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Cover photo: Eukoenenia maquinensis (Palpigradi: Eukoeneniidae), a new species from a Brazillian cave. Photo by Rodrigo Lopes Ferreira

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The effects of predation risk on female silk deposition and male response to predator-cued conspecifics in the wolf spider, *Pardosa milvina* (Araneae: Lycosidae)

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Abstract. Female *Pardosa milvina* (Hentz 1844) wolf spiders advertise sexual receptivity toward males via silk draglines, and male *P. milvina* exhibit conspicuous courtship behavior when encountering silk from females. Previous studies suggest that female *P. milvina* may benefit by limiting silk advertisements and excreta deposition when encountering silk from the predator, *H. helluo*, and male *P. milvina* may exhibit corresponding reductions in courtship when encountering silk from conspecific females previously exposed to *H. helluo* silk. We tested these predictions by comparing the amount of silk and excreta deposited by unmated female *P. milvina* exposed or not exposed to predator cues (silk and excreta) from *H. helluo*. We also measured and compared male *P. milvina* courtship latency and intensity in the presence of silk from females previously exposed or not exposed to predator silk from *H. helluo*. Contrary to predictions, we found a significant increase in excreta, dragline, and attachment disk deposition after females were exposed to *H. helluo* cues. Male *P. milvina* courtship latency did not vary among treatments despite increases in female silk deposition, but males significantly decreased courtship intensity when exposed to silk from females under predation risk. Vertical climbing to escape the predator cues may cause an increase in female silk deposition.

Keywords: Dragline, kairomone, pheromone, chemical cue, courtship

Conspicuous ornamentation and courtship displays of male wolf spiders increase mating success by attracting females and provide information about species identity (Stratton & Uetz 1986; McClintock & Uetz 1996; Scheffer et al. 1996; Parri et al. 1997; Hebets & Uetz 1999, 2000). However, elaborate ornaments and complex displays may incur considerable fitness-related costs because of their potential to draw the attention of nearby predators (Kotiaho et al. 1998; Pruden & Uetz 2004; Roberts et al. 2007; Hoefler et al. 2008). Consequently, males may benefit by reducing their overall activity level, including courtship intensity and duration, when under predation risk (Kotiaho et al. 1998; Taylor et al. 2005; Hoefler et al. 2008).

Female wolf spider dragline silk is an important medium for sexual communication (Kaston 1936; Hegdekar & Dondale 1969; Richter et al. 1971; Dondale & Hegdekar 1973; Tietjen 1979; Hebets & Uetz 1999; Rypstra et al. 2003; Schultz 2004; Gaskett 2007) and often serves as an advertisement to males. Although the predation costs associated with conspicuous male displays have been studied in a number of wolf spider species (Kotiaho 1998; Hebets 2005; Roberts et al. 2007; Hoefler et al. 2008), what remains less appreciated is that female silk may be chemically conspicuous to predators and increase predation risk as well, particularly among predators that use silk as a mode of communication. Consequently, females may benefit by reducing or modifying their silk advertisements toward males when aware of the presence of a predator.

A number of studies demonstrate that the wolf spider *Pardosa milvina* (Hentz 1844) can detect fine differences in predation risk through silk and excreta cues left by the larger predatory wolf spider, *Hogna helluo* (Walckenaer 1837), and respond with graded reductions in activity proportional to the perceived risk. *Pardosa milvina* can determine how recently *H. helluo* was in the area (Barnes et al. 2002), its diet (Persons et al. 2001), its hunger level (Bell et al. 2006), and the quantity of silk and excreta present (Persons & Rypstra 2001). Such discriminatory facilities suggest that *P. milvina* has sophisticated chemoreceptive abilities and that there is strong selection for recognition and evaluation of varying levels of predation risk.

Female *Pardosa milvina* exposed to *H. helluo* silk and excreta reduce activity (Persons & Rypstra 2001) and increase vertical orientation and climbing behavior (Persons et al. 2002; Folz et al. 2006). Exposure to these same cues can change foraging patterns to such an extreme that it directly affects body condition, prey capture behavior, and egg sac production of females, ultimately affecting the direct fitness of the spider (Persons et al. 2002). When in the presence of conspecific adult females, male *P. milvina* respond to *H. helluo* cues by delaying courtship (Taylor et al. 2005). In addition, *H. helluo* is attracted to silk and excreta produced by female *P. milvina* when they have been fed a diet of *P. milvina* (Persons & Rypstra 2000).

Given the potential predation costs associated with female silk advertisements, we addressed two questions: 1) Do female *P. milvina* alter the quantity and type of silk they deposit while in the presence of silk cues from the predatory wolf spider, *H. helluo*?; 2) Do male *P. milvina* respond differently to silk cues from female *P. milvina* that were under predation risk, without being exposed to the predator cues themselves? We predicted that female *P. milvina* would reduce their silk deposition or possibly pheromones associated with the silk when detecting chemical cues produced from the predator, *H. helluo*. If females reduce chemical advertisements toward males when

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under predation risk, then males should also show corresponding reductions in courtship behavior when detecting female silk deposited while the female was detecting a predator in the area, even when the male has no direct access to the predator's cues.

METHODS

Spider collection.—Subadult female *H. helluo* and *P. milvina* were collected in agricultural fields near the campus of Susquehanna University, Selinsgrove, Pennsylvania, Snyder County, USA. To assure the virginity of test spiders, we allowed all spiders to mature in the laboratory. The *P. milvina* were maintained in 0.074 l translucent containers (8 cm diameter, 5 cm height) and *H. helluo* were maintained in 0.473 l (9.8 cm diameter, 8.5 cm height) plastic deli dishes. Each spider was given water ad libitum and fed a diet of juvenile (ca 0.25 cm) domestic house crickets (*Acheta domesticus* Linnaeus) for *P. milvina*, and adult house crickets for *H. helluo*. All spiders were fed 2–3 crickets every 3–4 days, and then fed to satiety 1–2 h before testing to minimize the effects of body condition and hunger level on silk production and male courtship. We only used spiders that had finished feeding at the time of testing.

General experimental protocol.—We collected data relevant to each question with a separate protocol and a different set of males and females. Males in the second protocol and females in both protocols were tested twice, once under conditions of predation risk and once under conditions of no predation risk. We randomized the order of exposure such that half of the test spiders were subjected to the predation risk treatment first while the other half were exposed to the "no predator cue" treatment first. This was done to minimize any confounding effect of experience or other associated sequence effect. We analyzed female silk and male courtship behavior using paired *t*-tests, with predator risk and no risk as independent variables. We conducted tests in September–December, 2006.

Quantifying silk deposition.—We randomly chose 30 adult, laboratory-reared, virgin female *H. helluo* and used them in both parts of the experiment to deposit predator cues for multiple treatments. We placed each female *H. helluo* in a clean, 0.473 l white plastic testing container (9.8 cm diameter, 8.5 cm height) for four hours on a black paper substrate (9.8 cm diameter) printed with a grid to allow us to quantify silk production. Each substrate was divided into a grid of 3 mm × 3 mm sub-squares (approximately 766 squares). In a second control treatment, we used no predator stimulus in the container but the container setup was otherwise identical. Once the *H. helluo* was removed, we examined each paper substrate for the presence and amount of silk under a dissecting stereomicroscope. Silk types included attachment disks, which were discrete butterfly or u-shaped strands of silk produced by the piriform glands, and thin linear dragline silk produced by the ampullate silk glands (Richter et al.1971). Each grid sub-square was then scored from 0–4 based on the percentage of the area covered by silk (0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%). We also counted the total number of drops of excreta and attachment disks across the entire grid surface. *Hogna helluo* silk served as a predator stimulus for female *P. milvina*. We quantified *H. helluo* silk and excreta prior to the introduction of the female *P. milvina* in order to calculate the amount of *P. milvina* dragline silk, excreta, and attachment disks. For control trials, we quantified *P. milvina* dragline silk, excreta, and attachment disks alone, with no predator stimulus.

After each grid was scored, we placed a laboratory-reared, virgin, female *P. milvina* in the container for four hours to deposit cues on top of the *H. helluo* silk and excreta or on the blank substrate in control trials. *Hogna helluo* cues were scored within one–two hours of deposition before a female *P. milvina* was placed on the cues. After scoring the first two sets of 15 replicates per treatment (n = 30), we reversed the treatments and ran them a second time. After running female *P. milvina*, we scored the grids a second time, subtracting the initial *H. helluo* silk score to estimate female *P. milvina* silk deposition.

Quantifying male *Pardosa milvina* courtship behavior.—To measure the effects of the context in which female silk was deposited on male courtship behavior, it was necessary to separate the cues of the predator *H. helluo* from those of the female *P. milvina* exposed to the predator cues (Fig. 1 A, B). In a clean, 0.473 l container, we placed a single adult, laboratory-reared, virgin female *H. helluo* on a blank white paper substrate for four hours to deposit cues. We then removed the female *H. helluo*, and inserted another 0.473 l dish with the bottom completely removed (a circle of 8 cm diameter), save for an approximately 9 mm rim around the bottom, into the original container. We placed an unmated laboratory-reared adult female *P. milvina* on the substrate in the presence of predator cues with the inserted dish for four hours. No food or water was provided during this time period. We then removed the inserted dish and wiped the bottom with a small amount of ethanol to deactivate and remove any remaining predator cues. After the ethanol had evaporated, we placed the insert in a clean dish with a male *P. milvina* and documented courtship behavior for 30 minutes while the male was exposed to only the female conspecific cues on the 9 mm rim. We ran an identical treatment without the initial presence of *H. helluo* cues (Fig. 1 B). In both treatments, the male was responding solely to the conspecific female silk. As in the protocol for females, both treatments were conducted with the same set of 24 male subjects, assigned randomly to first experience cues from either females with or females without exposure to a predator. We used paired *t*-tests to compare female silk deposition with and without predator cues. We also used paired *t*-tests to compare male courtship latency and courtship intensity across treatments.

We defined courtship in *P. milvina* as a combination of two separate and distinct behaviors, leg raises and body shakes. A leg raise is raising the first pair of legs in unison above the cephalothorax and bringing them down abruptly. A body shake is a set of rapid oseillations of the abdomen and cephalothorax, often in conjunction with a leg raise. These behaviors have been described elsewhere and are known to influence female mate choice (Montgomery 1903; Kaston 1936; Brautigam & Persons 2003). Courtship latency constitutes the time elapsed between when a male was first placed on the substrate and when he began courtship (either with a leg raise or a body shake). We measured courtship intensity as the sum of body shakes and leg raises divided by courtship duration.

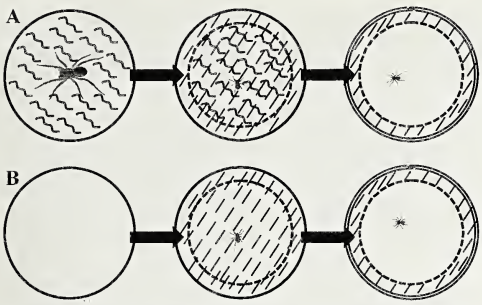

Figure 1.—Experimental containers for measuring behavioral response in male *P. milvina* with (A) and without (B) *H. helluo* silk present during female *P. milvina* silk deposition. A. An adult female *H. helluo* is allowed to deposit silk and excreta on the bottom of a container for 4 hours. A second clean container with the bottom removed (except for a shallow lip along the edge) is nested within the predator-cued container. A single unmated female is then allowed to deposit silk for four hours on top of the predator cues within these two nested containers. The inner container is then removed, the bottom cleaned, and nestled into a clean container devoid of predator silk. A single male *P. milvina* is then introduced into the container and its courtship behavior is quantified. Note that males have access only to silk that females deposited while they detected *H. helluo* chemical cues, but that the males have no silk cues available from *H. helluo* directly. B. The same procedure as in A is followed, except female *P. milvina* do not perceive predator cues during silk deposition.

RESULTS

We found that when exposed to cues (silk and excreta) from the larger predatory wolf spider *Hogna helluo*, female *Pardosa milvina* showed a significant increase in deposition of both silk and excreta. When we exposed male *P. milvina* to conspecific cues from females exposed to predator cues, we found that males significantly decreased courtship behaviors and courted significantly less intensely.

Effects of predator cues on female silk deposition.—There was a large increase in total dragline silk (paired $t = 2.449$, $P = 0.0206$), attachment disks (paired $t = 2.708$, $P = 0.0112$) and excreta (paired $t = 2.574$, $P = 0.0154$) from female *P. milvina* when exposed to *H. helluo* cues (Fig. 2 A–C).

Effects of predator-cued female silk on male courtship behavior.—There were significant decreases in male courtship behaviors when exposed to predator-cued, conspecific females. During courtship, males dramatically decreased the total number of body shakes, the intensity of leg raises and the intensity of body shakes when exposed to cues from females under predation risk (Table 1 for all behaviors). Total courtship intensity (leg raises and body shakes/courtship duration) also decreased among males exposed to predator-cued conspecifics (Table 1). Total leg raises showed a qualitatively similar decrease, but the decrease was not statistically significant (Table 1).

DISCUSSION

Our results clearly show that female *P. milvina* produce greater quantities of silk, excreta and attachment disks in the presence of predator cues from *H. helluo* and that in some

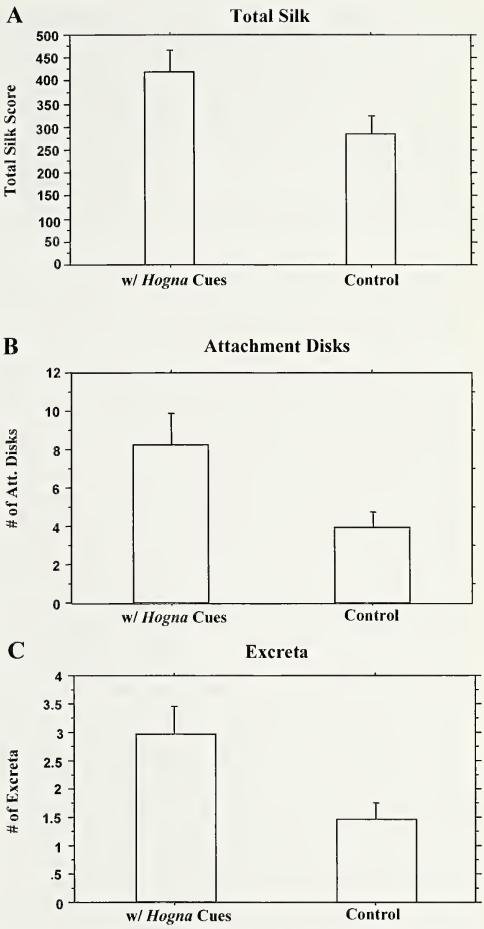

Figure 2.—Female *Pardosa milvina* silk and excreta deposition with and without silk from a predator present. A. Total silk score was calculated as the cumulative sum of all the sub-squares of each grid. Each grid square was scored from 0–4 based on an approximate percentage of the area of the square that was covered by silk. The total possible score if all grid squares were completely covered with silk would be 3064 (see text for more details). B. Deposition of female *P. milvina* attachment disks and C. Excreta. Unlike with the scoring method for total silk, each drop of excreta and attachment disk were discrete and were therefore counted directly.

manner, a potential predator can indirectly affect the behavior of a male even though the male has no direct access to predator cues. Several studies have examined the effects of conspicuous courtship displays of wolf spiders on the probability of attacks from nearby predators (Kotiaho et al. 1998; Pruden & Uetz, 2004; Roberts et al. 2007), but to our

Table 1.—Measures of male courtship behavior (mean ± S.E.) in response to female silk deposited while the female was exposed to *H. helluo* silk and excreta or control treatments without *H. helluo* cues. *P*-values are based on paired *t* tests. See text for definitions of courtship behaviors.

Behavior	Treatment		*t*	*P*
	w/ *Hogna* cues	Control		
Leg raise number	21.33 ± 5.2250	46.79 ± 15.005	1.917	0.0677
Body shake number	2.54 ± 0.8470	12.08 ± 4.125	2.718	0.0123
Leg raise intensity	0.0123 ± 0.0030	0.0279 ± 0.008	2.135	0.0436
Body shake intensity	0.00148 ± 0.0005	0.00699 ± 0.002	2.770	0.0109
Total courtship intensity	0.0137 ± 0.0030	0.0349 ± 0.011	2.318	0.0297

knowledge, this is the first study documenting that male courtship behavior can be modified in direct response to the predation context of female silk deposition.

Female silk deposition increased while under predation risk, yet male courtship intensity significantly decreased when encountering silk from a conspecific female that had previously detected predator silk. This surprising result runs counter to several of our predictions. When adult *H. helluo* have been reared on a diet of *P. milvina*, they preferentially choose to forage in areas where adult female *P. milvina* silk and excreta cues are present (Persons & Rypstra 2000). This suggests that females that deposit greater quantities of silk may attract *H. helluo*. If a female is under perceived predation risk, then it may be adaptive to limit the amount of silk deposited to reduce attracting predatory wolf spiders. We might then expect that reductions in silk would lead to an impaired ability of males to detect females, which would translate into increased courtship latency and less intense courtship. However, our results showed that females significantly increased total silk deposited, attachment disks, as well as excreta when under perceived predation risk.

The females that were exposed to a potential predator's cues could be engaging in a number of different anti-predator tactics. Female *P. milvina* increase climbing behavior and attempt to move up the side of a container when the horizontal substrate contains silk and excreta from *H. helluo* (Persons et al. 2002; Folz et al. 2006). This behavior would likely require a greater number of attachment disks as a means of anchoring the spider while climbing. If so, climbing females may release significantly more silk in an effort to escape the container. Alternatively, increased deposition of silk may simply be a non-adaptive reflexive response to an acute stressor such as the presence of predator cues.

Excretion increased in the presence of predator silk as well. Excretion in the presence of a predation threat is known to be an effective anti-predator response for a number of arthropods by either increasing locomotor efficiency or repelling potential predators (Weiss 2006). It is possible that *H. helluo* silk caused *P. milvina* to avoid the center of the container, resulting in proportionally more time spent exhibiting thigmotaxis (wall-hugging). We suggest this is unlikely, however, since numerous studies have shown that female *P. milvina* spend significantly more time on *H. helluo*-cued substrates due to freezing responses. Anecdotal observations of spider dragline deposition suggest that deposition rate is a function of time spent moving. Given that numerous studies have shown that female *P. milvina* locomotion decreases in the presence of *H. helluo* cues (e.g., Persons et al. 2001; Persons & Rypstra 2001), it suggests that the deposition rate must dramatically increase as a proportion of time spent moving.

The fact that adult males reduced courtship when detecting larger quantities of female silk suggests that there is not a simple positive relationship between the quantity of female silk and male courtship intensity. If anything, our results indicate a negative relationship between these variables. The relative importance of the tactile component of silk versus sex pheromones perfused on silk remains unknown. At least some wolf spider species respond to silk cues that are devoid of pheromones (Tietjen 1977; Tietjen & Rovner 1982), while other wolf spiders, such as *P. milvina*, are able to produce airborne pheromones that induce responses in males independent of male contact with silk (Searcy et al. 1999). Our results suggest that females could have reduced sex pheromone deposition on the silk even while increasing the amount of silk. If *H. helluo* attraction to female *P. milvina* is based on these pheromones rather than silk, increased silk deposition would have little consequence in attracting *H. helluo*. Also, the strength of *H. helluo* preference for cues associated with *P. milvina* may not necessarily be dependent on the quantity of *P. milvina* silk or excreta, but only on the presence or absence of these cues.

Regardless of the proximate cue used to elicit courtship behavior in males, our study provides indirect evidence that qualitative differences in the silk may be more important than quantitative differences in mediating male courtship displays. *Pardosa milvina* appears to produce at least two discrete types of dragline silk, heavy gauge cord silk and fine gauge dragline silk, which has a diameter approximately ten times smaller than heavy gauge silk. The ratio or quantity of these two silk types could vary markedly with and without predator cues, and each silk type may convey different information to males.

One hypothesis that could explain the significant decrease in several male courtship behaviors is that there is a change in the cues deposited among the females when under predation risk. Regardless of the specific source of the female stimulus, males appear capable of appropriately reducing courtship levels which, in turn, likely decreases the probability of predation. Since we know almost nothing about the quantitative relationship between sex pheromone production and silk production in lycosids, this explanation must remain speculative. However, given the sophisticated ability of *P. milvina* to extract a variety of information about predators from silk and excreta cues alone, we believe their chemoreceptive capabilities may be sufficiently advanced that an indirect transfer of

information about the presence of a predator is possible through conspecific female *P. milvina*. Additional studies that examine differences in predation risk based on the quantity of female silk deposited may prove fruitful.

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The visual system of the Australian wolf spider *Lycosa leuckartii* (Araneae: Lycosidae): visual acuity and the functional role of the eyes

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Abstract. Ocular arrangement and visual acuity were examined in *Lycosa leuckartii* Thorell 1870 (Araneae: Lycosidae), using histological techniques. Major structural and functional features of the visual system, including external and internal ocular organizations, resolution, sensitivity, focal lengths and the field of view, were characterized for each eye. *Lycosa leuckartii* had a large developmental investment in a specialized visual system with high visual acuity. The field of view extended 360° and displayed the potential for good depth perception. Anterior eyes showed average focal lengths (AL eyes 230.88 μm, AM eyes 276.84 μm), while the posterior eyes far exceeded them (PL eyes 499.26 μm, PM eyes 675.35 μm). Resolution of the anterior eyes was comparable to records in the literature for other lycosids (inter-receptor angle AL eyes 2.45°, AM eyes 1.85°), while the resolution of the posterior eyes was higher (PL eyes 0.78°, PM eyes 0.67°). Sensitivity of the lens (*f*-numbers) was highest in the secondary eyes and was close to some of the highest reported for Araneae (*f*-numbers PM eyes 0.58), but when receptor diameters were included in estimates, S-numbers were similar or lower than closely related species (PL eyes 17.5 μm^2, PM eyes 17.6 μm^2). There is a clear distinction in organization and function between the posterior and anterior eyes of *L. leuckartii*. The posterior eyes suit long- range predator and prey detection, while the anterior eyes are best for distance judgment and prey capture.

Keywords: Field of view, focal length, resolution, sensitivity

The modern arachnids are the only group of arthropods in which the eyes are camera-type, similar to our own, rather than compound eyes (Land 1985). Despite this, the structure and function of the visual system of spiders has been inadequately studied in many families of spiders when compared to chemo- and mechanoreception. This is likely based on the assumption that most spiders are nocturnal and vision may be of limited use (Foelix 1982). However, for some species, vision can be very important. Members from at least one family, the Salticidae, have been shown to hunt exclusively using vision (Jackson 1977), and members of five other families of spiders, Lycosidae, Pisauridae, Thomisidae, Oxyopidae and Deinopidae, show visually guided behaviors during locomotion, homing, prey capture, and courtship (Bristowe & Locket 1926; Kaston 1936; Whitcomb & Eason 1965; Robinson & Robinson 1971; Forster 1982; Uetz & Stratton 1982; Rovner 1996).

The visual acuity of a species is determined by characteristics of the eyes such as field of view, focal length, resolution, and sensitivity. The external placement and internal arrangement determine the field of view of each eye (Land 1985). The ancestral eye arrangement, as hypothesized by Homann (1971), consists of two transverse rows, each containing four eyes. The first row consists of the anterior median (AM) eyes in the middle and the anterior lateral (AL) eyes on the periphery. Similarly, the posterior eyes are grouped into posterior median (PM) eyes and posterior lateral (PL) eyes. The visual angle of the field of view for each eye can vary greatly, from relatively narrow pinpoint views of only 24° in the PL eyes of *Badumna insignis* Koch 1872 (Clemente et al. 2005) to 182° wide-angle views in the AM eyes of *Octonoba sinensis* Simon 1880 (Opell 1988). Forward-facing binocular vision is a product of overlapping visual fields, and is necessary for good distance judgment.

The distance over which an eye can focus upon an object is determined by the focal length of its lens (Homann 1971). This ranges from 38 μm in the AL eyes of the uloborid *Hyptiotes cavatus* Hentz 1847 (Opell & Ware 1987), to 448 μm in the PM eyes of *Cupiennius salei* Keyserling 1877 (Land & Barth 1992), up to 1980 μm in the AM eyes of the jumping spider *Portia* (Williams & McIntyre 1980).

The ability of the eye to resolve detail depends on the fineness of the retinal mosaic, usually expressed as the inter-receptor angle. The finer this angle, the better the resolution of the eye. The finest inter-receptor angles reported in the literature are for members of Salticidae, the diurnal jumping spiders, for which the inter-receptor angle in the AM eyes can be less than 1°. The largest angle reported for hunting spiders is 7° in the AL eyes of a lycosid species (Homann 1931; Land 1969, 1985).

Sensitivity, or the ability to see in low light levels, is a combination of the physical properties of an optical system and the physiological sensitivity of photoreceptors. The physical ability of the lens to admit light is often expressed in the literature as an *f*-number, which decreases with increasing sensitivity (Opell & Ware 1987). This ranges from 2.68–5.90 in diurnally active jumping spiders (Land 1969; Foelix 1982) to 0.58 in the PM eyes of the wholly nocturnal ogre-faced spider *Deinopis subrufa*, Koch 1879 (Blest & Land 1977). However, a more complete estimate of sensitivity is given by an S-number (Land 1981), which is a product of the relative aperture of the eye, determining the light flux passing through to the retina, the cross sectional area of the receptor, and the proportion of light entering a receptor that is actually

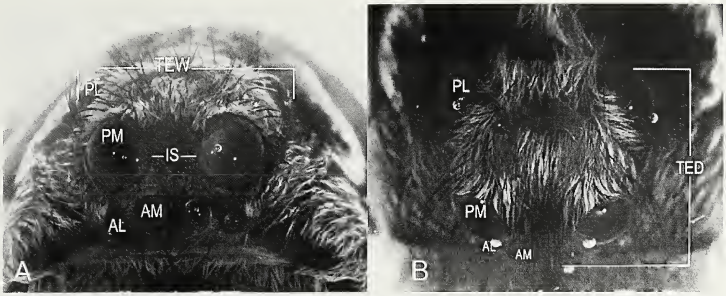

Figure 1.—External measurements taken on *L. leuckartii*. A = anterior view, B = dorsal view. AM, anterior median eyes; AL, anterior lateral eyes; PM, posterior median eyes; PL, posterior lateral eyes; TED, total eye diameter; TEW, total eye width; IS, interocular space.

absorbed by it. This has the advantage of increasing as sensitivity increases, and can range from 0.09 μm^2 in the AM eyes of jumping spiders to 387 μm^2 in the PM eyes of *Deinopis* (Land 1985).

Both resolution and sensitivity vary in relation to the light conditions under which species operate (Opell & Ware 1987). While resolution improves as the ratio of receptor diameter to focal length decreases, sensitivity improves as the same ratio increases. Therefore, in the structure of the eyes, there is a trade-off between resolution and sensitivity. The only solution to the trade-off is to increase the total size of the eye; therefore, total eye size can be an indicator of the relative importance of vision.

Many studies link various eyes to their probable role or relative use in prey acquisition (Uehara et al. 1978; Forster 1979; Kovoor et al. 1992; Rovner 1993; Schmid 1998; Ortega-Escobar & Munoz-Cuevas 1999). There are two important components of prey acquisition. The first is prey detection, which incorporates initial detection of an item, specifically distinguishing the item as prey, predator or conspecific, and some orientation and movement toward the prey item. Therefore, prey detection requires long-distance detection and image clarity. The second component is prey capture. This may involve some identification of prey or non-prey items and orientation toward the prey, but mainly comprises judgment of distance for accurate lunging and striking (Lizotte & Rovner 1988).

Previous studies have demonstrated that the visual system of lycosid spiders is particularly complex. The eyes of lycosids have intricate visual fields (Homann 1931), high resolution and sensitivity (Lizotte & Rovner 1988; Kovoor et al. 1992; Rovner 1993; Ortega-Escobar & Munoz-Cuevas 1999) and the ability to detect polarized light (Kovoor et al. 1993; Dacke et al. 2001; Ortega-Escobar 2006). However, much of this work has been performed on relatively few species of lycosids, and it is unclear how much variation exists within the family. A recent molecular phylogeny of lycosids has suggested that the family consists of several clades (Murphy et al. 2006). While much of the work on vision in lycosids has focused on Palaeartic and Nearctic species, the Australian species form a separate distinct clade. Almost no information is available on variation among clades. As a taxonomic aside, it is noted that the generic position of *Lycosa leuckartii* is currently under review by V.W. Framenau with a proposed reallocation of the species pending. We present details of the visual acuity of *Lycosa leuckartii* and compare them to other lycosids and other families of spiders.

METHODS

External ocular organization.—Twenty individual *Lycosa leuckartii* were used to record external measurements. These included total eye width (TEW), total eye depth (TED) and eye diameters (Figs. 1A & B). We took measurements under a binocular dissecting microscope with an eyepiece micrometer. The values were then standardized for the animals' size by dividing each measurement by the carapace length. A repeated-measures ANOVA with one within-subject factor and no between-subject factors, and Student-Newman-Keuls post-hoc test, were used to determine significant differences in the relative eye diameters.

Internal ocular organization.—Two specimens of *L. leuckartii* were killed, using CO_2 gas, trimmed to a small block of tissue and fixed in Karnovsky's fixative for at least 72 h. We then washed and further trimmed down specimens in spider saline (scorpion saline excluding the $CaCl_2$: Zwicky 1968) and placed them in phosphate buffer prior to their being embedded in araldite/procure. Longitudinal and transverse (frontal plane) sections (1 μm thin) were cut using an LKB ultratome and a diamond knife. We mounted sections on slides and stained them with toluidine blue. As well as determining the internal ocular organization, we also used these sections in measurements of resolution and sensitivity.

Focal length.—The focal length (*f*) of each lens was determined using the 'hanging drop' method described in Homann (1928) and Land (1985). The lens, along with a small proportion of the surrounding cuticle, was dissected from the head and stored in spider saline. After being cleared of excess tissue in warm, dilute, sodium hydroxide, the lens was suspended in a drop of spider saline from the underside of a cover slip. Using a microscope, we then viewed the image through the lens, targeting an object of known size (o). The distance between the slide and the object was then measured using calipers (u). The size of the image (i) was ascertained, using calibrated digital images, and the focal length was

calculated, using the formula (1) described by Opell & Ware (1987):

$$f = (i/o)\ (u) \quad (1)$$

For each lens type, we determined an average of the values measured. Repeated-measures ANOVA, with one within-subject factor (eye) and no between-subject factors, with a Tukey-Kramer post-hoc test, were used to determine differences between the focal lengths of the different eyes.

Sensitivity.— Sensitivity (*f*-number), or the eye's ability to admit light, was calculated using values for focal length (*f*) and the diameter of the retina (*d*), measured from the extremities of the rhabdomeres in each species (Opell & Ware 1987). We determined focal lengths by the above methods and ascertained retinal diameters by taking measurements from slides obtained using methods described for internal ocular organization. These values were then entered into the sensitivity equation (2) outlined in Opell & Ware (1987):

$$f\text{-number} = f/d \quad (2)$$

The sensitivity of the eye can also be given in terms of an S-number, as described by Land (1985). Here sensitivity is defined, not only by the relative aperture of the eye, but also by the cross sectional area of the receptor and the amount of light absorbed by the receptor, as shown in equation (3):

$$S = (\frac{\pi}{4})^2 (\frac{D}{f})^2 (d_r^2)(1 - e^{-kl}) \quad (3)$$

where D is the diameter of the lens, f is the focal length, d_r is the receptor diameter (assumed to equal the center-to-center spacing of the receptors), l is the length of the receptor and k is the extinction coefficient of the photopigment in the receptors. Following Land (1981, 1985) k was approximated to be 0.0067 for rhabdomeric photoreceptors, and l was multiplied by 2 in the secondary eyes as the reflective tectum may allow photons to bounce back past the receptor, effectively lengthening it.

Resolution.—We counted the numbers of axons exiting each eye from sections cut using the same methods as for internal ocular organization. Resolution is dependent upon the number of photoreceptors, or rhabdomeric cells per eye. The higher the density of cells, the finer the resolution of an image (Land 1985). The number of nerve axons exiting a spider's eye is in a 1:1 ratio with the number of photoreceptors (Uehara & Uehara 1996). To compare the density of visual cells per eye, we figured the inter-receptor angle ($\Delta\phi$) based upon Land (1985) as given by equation (4):

$$\Delta\phi = \frac{d_{cc}}{f} \quad (4)$$

where d_{cc} is the center-to-center spacing of retinal receptors and f is the focal length. The inter-receptor angle was calculated by measuring the pigment ring diameter of the retinal mosaic from histological sections and using the average maximum visual angle from the field of view (see below) to calculate the total area of the retinal mosaic. This was divided by the total numbers of photoreceptors per eye to give an estimate of receptor area, and hence diameter. Retinal diameter was assumed to equal d_{cc} based on Land (1985).

Table 1.—Optical data and sensitivities of the eyes of *Lycosa leuckartii*. Where multiple measurements were taken, mean plus standard error is shown. D = diameter of the lens, f = focal length, d_{cc} = center to center spacing of the photoreceptors, f = number as calculated in Equation 3. S-numbers, as calculated in Equation 3, are shown based upon the length of the tapetum. S-numbers based on 2× length of the tapetum are shown in parentheses.

Eyes	D μm	f μm	d_{cc} μm	f-number	S-number μm²
AM	292 ± 10.4	276.84 ± 16.89	8.93	1.08	-
AL	230 ± 8.4	230.88 ± 5.74	9.87	0.69	-
PM	752 ± 21.9	675.35 ± 56.19	7.96	0.56	9.82 (17.6)
PL	647 ± 18.7	499.26 ± 13.40	6.81	0.75	9.72 (17.5)

Field of view.—We used a Welch Allyn medical ophthalmoscope, along with an Aimark perimeter arc (153 mm diameter) constructed for use on spiders, to determine the extent of visual fields for *L. leuckartii*. A freshly killed *L. leuckartii* was utilized, and measurements were taken in a darkened room, using the light reflecting from the tapetum to determine limits of the fields of view of each eye. We moved the ophthalmoscope around the perimeter arc, viewing the bright green reflection from the tapetum of the secondary eyes, or the dull red reflection from the rhabdomeres of the primary eyes. Readings were taken on the perimeter arc at every 10° from horizontal, and were plotted directly onto a Geological Stereonet by rotating the stereonet 10° between each point. A stereonet is typically used to plot three-dimensional angles in two dimensions and, similar to the Aitoff equal area projection (utilized by Land & Barth 1992), the resultant plot represents 180° of a globe at infinity with the spider at the center. Average maximal visual angle (AMVA) was calculated by averaging the maximum horizontal and vertical arcs.

Representative specimens from the study population along with slide preparations are held in the Zoology Building, School of Animal Biology, University of Western Australia.

RESULTS

External ocular organization.—The average carapace length of *L. leuckartii* was 826 μm. *Lycosa leuckartii's* eyes appear to form three rows. The first of these is similar to the ancestral arrangement, a single row consisting of the AL and AM eyes. With subtle evolutionary modifications, the PL eyes have moved around and back to form a row separate from the central row of the PM eyes. These modifications result in the total eye width being similar to total eye depth (TEW = 247 ± 4.8 μm; TED = 221 ± 4.4 μm).

For the *Lycosa leuckartii* specimen, all pairs of eyes showed significant differences in diameters from one another ($F_{19,3}$ = 406.9, $P < 0.001$), the forward facing PM eyes had the largest diameter, closely followed by the obliquely oriented PL eyes, and then the AM and AL eyes (Table 1).

Internal ocular organization.—The AM eyes display a typical bi-convex lens formed by a visible thickening of the cuticular layer. The lens is separated from the retina by a layer of columnar vitreous cells. The retina is composed of visual cells and pigment cells. The most anterior portion of the visual cell, which contains the rhabdomeres, borders the vitreous

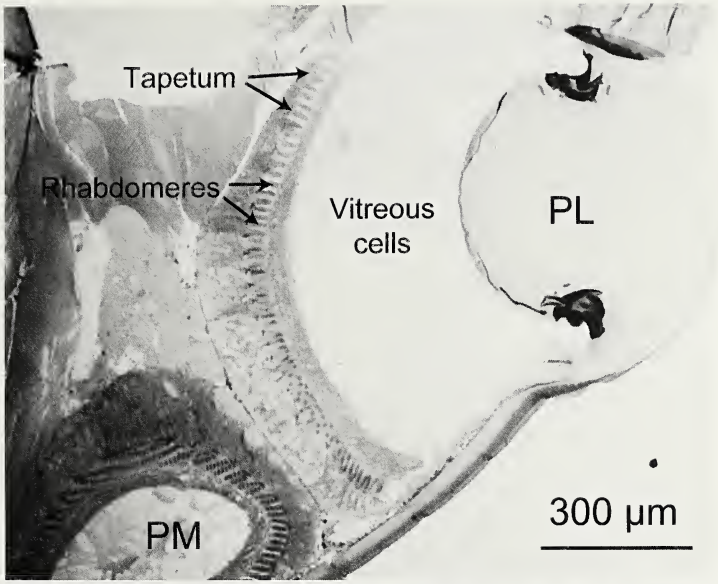

Figure 2.—Structure of the posterior lateral eye (PL) and the posterior medial eye (PM) of *L. leuckartii*, in a transverse section of the prosoma.

layer, and the nuclei lie below. The secondary eyes of *L. leuckartii* have a distinct 'grid-shaped' tapetum (Fig. 2). A thin dark layer of visual cells containing the rhabdomeres separates the vitreous cells and the tapetum. The length of the tapetum measured directly from cross-sections averaged 31.75 and 32.22 μm long for the PL eyes and the PM eyes, respectively.

In the anterior eyes of *L. leuckartii*, one discrete nerve bundle was found to emerge from each eye, but the posterior eyes produced multiple bundles of nerve axons. These emerged from various points around the perimeter of the eyecups and moved through the middle of the prosoma toward the supra-esophageal ganglion (Fig. 3). The PL eyes together gave rise to 18 bundles of axons. Each contained from 92 to 987 nerve axons per bundle. The PM eyes together generated 35 bundles. Each of these contained from 30 to 728 nerve axons per bundle.

Focal length.—There were significant differences in the focal lengths of the four pairs of eyes in *L. leuckartii* ($F_{1,3} = 42.4$, $P = 0.006$; Table 1). A Tukey-Kramer post-hoc test revealed that there were significant differences between the anterior and posterior pairs of eyes. Both pairs of anterior eyes had similar focal lengths (average = 253.86 μm). The posterior eyes were similar to each other, but showed much longer focal lengths than the anterior eyes (average = 587.30 μm). Direct inspection of the image produced by the lens showed that it was of good quality and therefore not subject to spherical aberration (Fig. 4).

Sensitivity.—Based upon *f*-numbers, the highest sensitivity for *L. leuckartii* was found in the PM eyes. The other secondary eyes of *L. leuckartii* (PL and AL) also displayed similarly low *f*-numbers, indicating high sensitivity (Table 1). The highest *f*-number in *L. leuckartii* was found in the AM eyes, suggesting it has lower light sensitivity than the secondary eyes. S-numbers calculated for the PL eyes were similar to estimates for S-number of the PM eyes (Table 1).

Resolution.—The optic nerves from all four pairs of eyes of *L. leuckartii* were found grouped together, surrounded by muscle along the midline of the prosoma. Identification of which nerve bundles originated from the left and right anterior eyes was possible by observing the arrival sequence (within the slides) of each nerve bundle and the direction from which it originated. The multiple nerve bundles originating from the posterior eyes of *L. leuckartii* could be distinguished as belonging to the PM or PL eyes, but could not be further separated into left and right eye nerve bundles; thus, total counts were made and half of this attributed to each eye.

The posterior eyes of *L. leuckartii* gave rise to approximately 12 times the number of nerve axons seen in the anterior eyes (Table 2). Receptor diameters were larger for the anterior eyes (average = 9.4 μm) when compared to the posterior eyes (average = 7.4 μm; Table 1). Accounting for eye size and visual fields, we concluded that this translated into greater resolution, the inter-receptor angle for the posterior eyes being less than a third that of the anterior eyes (Table 2). This appears to be below the potential resolution of the eyes. Following Land & Barth (1992), we discovered that the ultimate limit to resolution is determined by the blur resulting from diffraction at the aperture, given by $57.3w/D$ deg, where w is the wavelength of light (assumed to be 0.5 μm) and D is the diameter of the lens. This results in potential grating

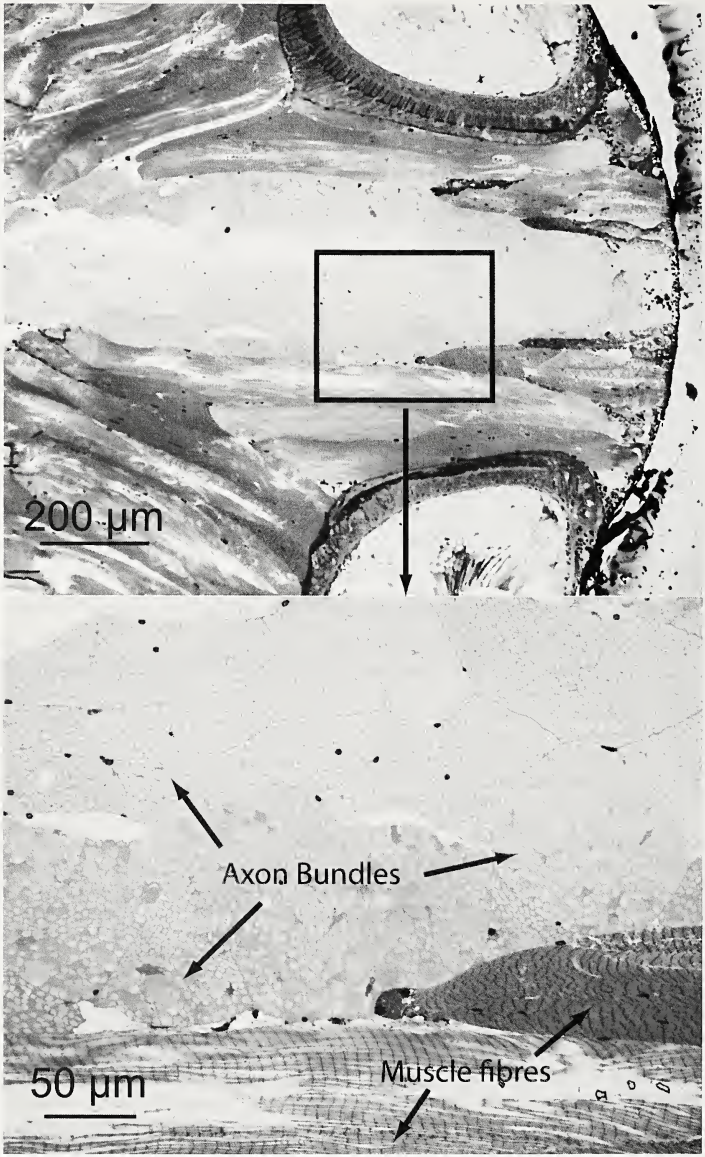

Figure 3.—Multiple nerve bundles of the posterior eyes of *L. leuckartii*. Upper panel = 10× magnification in transverse section; Lower panel = magnified (100×) view of the enclosed area above showing the discrete nerve bundles.

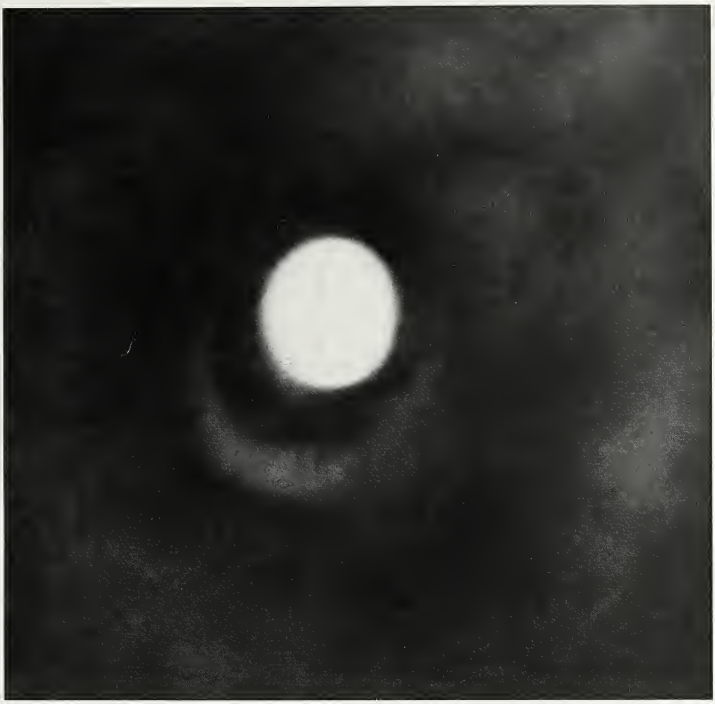

Figure 4.—View through the lens of *L. leuckartii*, suspended from a drop of saline underneath a glass cover-slip. The image is focused on two parallel lines.

periods between 0.12° (AL eyes) and 0.04° (PM eyes), which are an order of magnitude smaller than the inter-receptor angles measured, suggesting diffraction does not limit resolution.

Field of view.—Visual fields for *L. leuckartii* (Figs. 5A & B) were found to extend 360° around the animal, with a large overlap within 70° of the center. The PL eyes provided 220° of peripheral vision along the horizontal meridian, extending around the animal's sides and overlapping behind the animal. AMVA of each individual eye was greater than 80° (Table 1) and up to 107.8° in the PL eyes. The other three pairs of eyes (AM, AL and PM) all had some degree of forward facing overlap, indicating the potential for good overall binocular vision. The PM eyes, while covering 120° vertical maximum and 140° along the horizontal meridian, did not greatly overlap (maximum overlap 7° between 0 to 10° above the horizontal). The AL eyes provided a large degree of overlap (maximum 57°), but their visual axis was directed well below the horizontal (maximum overlap at 42° below horizontal). The AM eyes had a potentially large amount of binocular vision, with a maximum overlap of 42° at 24 to 30° above the horizontal, and with overlap extending from 20° below to 60° above horizontal.

Table 2.—Optical data and resolution of the eyes of *Lycosa leuckartii*. *d* = diameter of the pigment ring, AMVA = average maximal visual angle, A_r = calculated area of the retina based upon AMVA, $\Delta\phi$ = inter-receptor angle based upon Equation 4.

Eyes	*d* (μm)	AMVA °	Nerve no. axons	A_r μm²	$\Delta\phi$ °
AM	255.7	82.4	476	29,797	1.85
AL	335.8	80.2	257	19,670	2.45
PM	1194.7	96.9	4848	241,208	0.68
PL	662.5	107.8	4423	160,871	0.78

DISCUSSION

The greatest differentiation of the eyes of *L. leuckartii* occurs between the posterior eyes and the anterior eyes, suggesting that these eyes play different roles in the visual system. This is most evident in the overlapping visual fields of not only the AL eyes with the PM eyes, as was shown by Homann (1931), but also of the AM and PM eyes (Fig. 5). The visual fields of the posterior eyes have large visual angles and cover an almost 360° view, while the anterior eyes appear to be focused forward.

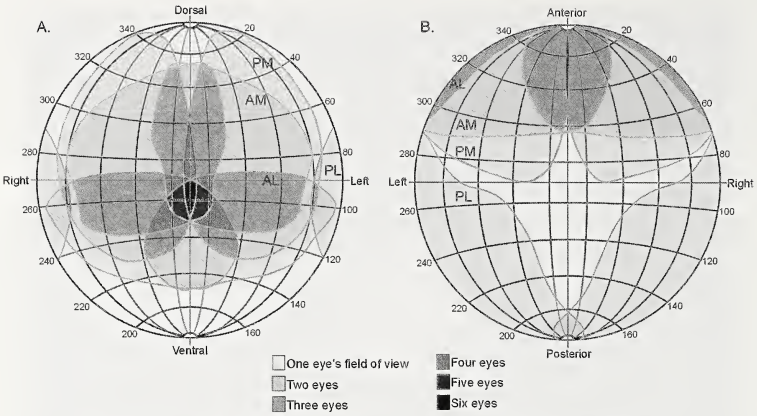

Figure 5.—Fields of view for *L. leuckartii*: A = frontal view; B = overhead view.

Differentiation in focal length is also evident between anterior and posterior eyes. These estimates of focal length can also be used to calculate the eye's depth of focus, which is the animal's nearest distance of clear vision. Following Land (1981), we determined that the nearest distance of clear vision (U) is given by $U = fD/2d_{cc}$, where f is the focal length, D is the diameter of the lens, and d_{cc} is the center-to-center spacing of the photoreceptors. This results in values for U of 4.5 mm for the AM eyes and 2.7 mm for the AL eyes. This is much less than the length of the legs, which suggests even the closest objects appear in focus. The posterior eyes, in contrast, have much larger U values of 32 mm (PM eyes) and 24 mm (PL eyes) and may therefore be of limited use at close range.

The posterior eyes also show potential for superior performance in both resolution and sensitivity, when compared to the anterior eyes. This implies that the posterior eyes may be best suited for long-range, wide-angle recognition of objects in low light conditions and would therefore be ideal for tasks such as prey detection. Similar predictions were reported based upon behavioral experiments on the lycosid spider *Rabidosa rabida* Walckenaer 1837 (Rovner 1993). When different combinations of eyes were occluded in *R. rabida*, spiders with usable PL eyes were able to perform sizable orientations (up to 160°) toward a stimulus, while the PM eyes were found essential for mediating long-range approaches toward the stimulus (Rovner 1993). This suggests the PL and PM eyes could determine the outer limits of the spider's visual perception and foraging patch.

In contrast, the short focal length and considerable binocular vision of the anterior eyes indicate good potential depth perception at short range, which may be an important component for short-range orientation and approaches during activities such as prey capture or courtship. This has been supported behaviorally for the AL eyes by Rovner (1993), but not for the AM eyes. However, a comparison of the roles of anterior eyes between *L. leuckartii* and *R. rabida* may be difficult, since the AM eyes are smaller than the AL eyes in *R. rabida*, while the opposite is true for *L. leuckartii* (AM eyes larger than AL eyes). This may signify a greater role in orientation, or more likely, approach, toward stimuli, for the AM eyes in *L. leuckartii*. Alternatively, the AM eyes have also been shown to play a role in orientation via polarized light (Magni et al. 1964, 1965; Magni 1966; Ortega-Escobar & Munoz-Cuevas 1999). Further, the AM eyes of *L. tarantula* Linnaeus 1758 also differ from the other eyes in having muscle attachments, and therefore better mobility (Ortega-Escobar & Munoz-Cuevas 1999). This led Land & Barth (1992) to conclude that one function of the AM eyes may be to analyze stationary objects, since small movements prevent the neural image from adapting, as occurs in the secondary eyes.

We observed a further distinction between the posterior and anterior eyes of *L. leuckartii* in the organization of the optic nerves. While each of the anterior eyes of *L. leuckartii* connects to one discrete nerve bundle, the posterior eyes exhibit multiple bundles (up to 35) exiting each eye. Multiple nerve bundles have previously been reported in another lycosid species. Researchers have found *Lycosa tarentula fasciventris* to have 20 nerve bundles exiting the PL eyes and 30 from the PM eyes (Kovoor et al. 1992). The function of multiple nerve bundles in the posterior eyes of *L. leuckartii* is not known. The presence of these discrete nerve bundles may be the result of developmental or functional differences and remains to be investigated.

The posterior eyes appear to have partially overcome the trade-off between resolution and sensitivity by increasing in size relative to the carapace. A comparison of the inter-receptor angle of the PL with other species of lycosid suggests that *L. leuckartii* has a much better resolution than *L. horrida* Keyserling 1877 (1.5–2.5°; Homann 1931), *L. singoriensis* Laxmann 1770 (= *Trochosa singoriensis*) (1.7–2.6°; Homann 1931) and two other species of *Lycosa* published in Homann (1931) (both 1.8°). Further, it appears that resolution for each eye of *L. leuckartii* is better than the corresponding eyes of that found in the closely related, nocturnal ctenid spider *Cupiennius salei* (Land & Barth 1992).

The sensitivity of the lens was also high for *L. leuckartii* when compared with other species. The least sensitive of the

eyes of *L. leuckartii*, the AM eyes, are comparable in *f*-numbers to nocturnally active web-building uloborids, whose *f*-number's range from 0.88–1.70 (Opell & Ware 1987). The sensitivity of the secondary eyes of *L. leuckartii* even closely approximates that of the PM eyes of the nocturnal ogre-faced spider *Deinopis subrufa* (*f*-number of AM eyes = 0.58: Blest & Land 1977).

When estimates of receptor size are included (S-numbers), the sensitivity for the PL eyes of *L. leuckartii* appeared twice as good as that of the PL eyes of a lycosid species reported in Homann (1931) and Land (1985); however, the S-number for the PL eyes of *L. leuckartii* was about ten times less than the PL eyes of *Cupiennius salei* (S-number 147 μm^2). This suggests that the visual system of *L. leuckartii* may be biased toward providing better resolution rather than sensitivity, though whether this translates into differences in performance remains to be investigated.

There appear to be important differences in the visual systems between Australian lycosids and Palaeartic lycosids. One possible source of this variation may be prey capture strategies. While most of the Australian lycosid species studied appear to be burrowing, the Palaeartic species are vagrant, or build temporary webs (Murphy et al. 2006). The quality of vision in one particular genus, *Pardosa*, should be examined, since this group appears to be predominately vagrant and may therefore show more reliance on vision. Nevertheless, there are a number of vagrant and web-weaving lycosids in Australia. Also a distinctive granite-rock-inhabiting genus in southern Western Australia, which shelters under exfoliated slabs on the rock surface and hunts in a vagrant fashion, is currently being described by Framenau et al. (in press) as a new genus. It certainly invites further research regarding its ocular capability.

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Possible functional significance of spigot placement on the spinnerets of spiders

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Abstract. This paper discusses the possible functional significance of the locations of the spigots of different types of silk gland on the different spinnerets of spiders. Deductions are based on recognition that some types of line are initiated by being attached to the dragline, that there is an anterior-posterior asymmetry in how such lines can be initiated, and that spigot location also affects the possibility of attaching lines to the substrate. Possible explanations are given for several morphological details, including the anterior location of the dragline, piriform and cribellum spigots, planar arrays of piriform and cribellum spigots, and posterior location of aciniform spigots. I argue that piriform gland products are not used to attach egg sac lines to each other, that sticky wrapping lines are initiated in theridiids and pholcids by attaching them to draglines and that lines from both aciniform and cylindriform glands are laid along with liquid that renders them sticky. The possible role of phylogenetic inertia in determining spigot locations is discussed. Further work is needed to determine whether termination of lines and accessibility of spigots for cleaning also influence their positions.

Keywords: Silk, silk gland, phylogenetics inertia

Spinneret morphology provides many useful taxonomic characters in spiders, and the distributions and forms of the spigots of different silk glands have been described for many species (summaries in Coddington 1989; Platnick et al. 1991; Agnarsson 2004; Griswold et al. 2005). Surprisingly however, there has been little discussion of the possible functional significance of the locations of spigots on spinnerets. Perhaps the most striking exception is the onchyroceratid *Ochyrocera cachote* Hormiga, Álvarez-Padilla & Benjamin 2007, which builds small domed sheet webs containing sectors with large numbers of precisely parallel lines (Hormiga et al. (2007). The posterior lateral spinnerets of *O. chachote* have an unusual row of tightly spaced aciniform spigots, and the similarity between the length of this row and the number of spigots with the width of the arrays of parallel lines and the numbers of parallel lines in the swaths (about 20) leave little doubt that each swath is produced during a single pass of the spider's spinnerets (Hormiga et al. 2007). Similar arrays of many parallel lines also occur in the webs of another *Ochyrocera* species in Costa Rica (G. Barrantes & W. Eberhard unpubl. results). A second case in which the possible functional significance of spigot positions on spinnerets has been discussed is the tight physical association between the spigots of the aggregate and the flagelliform glands in araneoid orb weavers, allowing the spider to coat the flagelliform line with sticky material from the aggregate gland as the line emerges from its spigot (Coddington 1987; Blackledge et al. 2009).

The present note combines direct observations and video recordings (30 frames/s) of the behavior of mature females of large araneoid species, data from the extensive literature on spinneret morphology, and data from the much less extensive literatures on how different types of lines are initiated and on their morphology (especially in the SEM) to propose possible functional explanations for the positions of a number of types of spigots in spiders. I argue that the sites of different spigots relative to each other influence the spider's ability to initiate and to coordinate the production of different types of lines, and that selection on these abilities may explain why particular spigots are located at particular sites. The arguments are not all complete, and the aim is to initiate discussions rather than to provide exhaustive, final answers.

General considerations regarding how lines are initiated and fastened.—Spigot placement probably affects how a spider can initiate lines. As is well known, spiders cannot eject silk lines, but must have them pulled from their bodies (Witt et al. 1968; Foelix 1996). Three different mechanisms have been proposed for line initiation. The best known, "direct contact" initiation technique occurs when the spider presses its spinnerets against a substrate and then pulls away (e.g., Kullmann 1975). If the spinnerets are held in appropriate positions, if the spigots are at appropriate sites on the spinnerets to bring their tips into contact the substrate, and if there is liquid silk at the tips of the spigots (they are "wet") (presumably due to abdominal pressure – Wilson 1962a), then this liquid will adhere to the substrate and the spider can initiate a new line when it pulls its spinnerets away. Similarly, lines could be initiated by direct contact between different spinnerets, with or without another line between them (see below).

A second way of initiating lines, "dragline initiation", was observed when *Nephila clavipes* (Linnaeus 1767) and *Argiope argentata* (Fabricius 1775) wrapped prey. For instance, when a large female *N. clavipes* begins to wrap a prey, the lines in the swath of wrapping lines (presumably from her aciniform gland spigots) are attached to her dragline (Fig. 1). The spider wraps the prey by snagging the wrapping lines with her legs IV and pulling out more silk by extending them toward the prey to press the wrapping lines against it. A second context in which dragline initiation occurs in a variety of species is initiation of airborne lines, when the distal ends of airborne lines are attached to the spider's dragline as it descends (Eberhard 1987) (in this case, the glandular origins of the lines are unknown). Initiation of these wrapping and airborne lines presumably occurs when the spider applies the "wet" tips of the spigots that produce these lines to a dragline while the dragline is being pulled as the spider moves.

This dragline initiation technique is only feasible if the spigots of different glands are aligned on the spinnerets in

Figure 1.—A swath of aciniform lines is attached to the dragline of a mature female *Nephila clavipes* as she descends, just before she initiates prey wrapping (drawn from a video recording).

certain ways. Spiders almost always move forward rather than backward while spinning draglines, so lines from spigots on the "downstream", posterior median and posterior lateral spinnerets (e.g., the aciniform spigots in araneoids) can be initiated using lines from spigots on the "upstream", anterior lateral spinnerets (e.g, dragline or major ampullate spigots). Movements of more posterior spinnerets in an anterior direction, and manipulations of lines with the legs can relax these constraints somewhat (see description of *Nephila* behavior below). The short lengths of most spinnerets, however, suggest the general rule that spigots that are located farther posterior on the spider's body (more downstream) can initiate lines by touching their tips to lines from more anterior (upstream) spigots, but not vice versa.

A final possible mechanism for initiating lines, "clapping initiation", involves spreading movements of the spinnerets with respect to each other (Blackwell cited in McCook 1889; Nielsen 1931; Eberhard 1987). For example, the spider could clap or rub pairs of spinnerets together, and then pull them apart. The spider could then either pull further silk with its legs, or use friction with the air to elongate the short lines between the spinnerets. Although there are reports that spinnerets are spread widely when some lines (e.g., airborne lines) are being initiated (Blackwell in McCook 1889; Eberhard 1987), I know of no confirmed demonstration of clapping initiation.

One further aspect of "upstream – downstream" locations concerns the use of one type of silk to fasten lines of another type of silk to the substrate or to other lines. The spigots of the fastening silk need to be either at the same level or downstream of the spigots that produce the lines that are being fastened.

Possible functional significance of spigot placements.—The placements of spigots on the spinnerets could alter the feasibility of all three possible types of initiation, and their observed positions may possibly be explained in terms of functional consequences. I will discuss possible functions according to the probable glandular origin of the lines.

Ampullate gland spigots: As far as I know, the only technique that has been observed in dragline initiation (which is relatively rarely observed in the many species that produce draglines more or less continuously) is direct contact (e.g., Kullmann 1975 on an unspecified species; W. Eberhard unpubl. results on *Micrathena duodecimspinosa* (O. Pickard-Cambridge 1890) when they initiate the dragline after finishing construction of the sticky spiral). The rather basal position of the major ampullate spigots on the anterior lateral spinnerets of many species (Coddington 1989) (Fig. 2) probably obliges the spider to either spread these spinnerets widely, or to insert the substrate (e.g., another line, the spider's tarsus) deep between them. I know of no direct observations, however, of this detail. Kullmann (1975) noted that dragline initiation can occur by contact even when the spider is anesthetized.

Aciniform gland spigots: As noted above, initiation of aciniform wrapping lines in araneoids apparently occurs using the dragline initiation technique (Fig. 1). The downstream placement of the aciniform spigots (on the posterior median and lateral spinnerets) (Fig. 2) in araneomorph spiders in general (Griswold et al. 2005) with respect to the major ampullate spigots may function to allow initiation of aciniform wrapping lines by attachment to draglines. The downstream placement of aciniform spigots in mygalomorph spiders and presumably on the common ancestor of all spiders must have a different explanation, however, as these spiders lack dragline silk (Palmer et al. 1982; Palmer 1985; Blackledge et al. 2009). The arrangements of the aciniform spigots of some mygalomorphs in a line along the long axis of the long posterior lateral spinneret (Peters 1967) is apparently an ancient trait (Vollrath & Selden 2007). Similar linear arrays of aciniform spigots also occur in other groups with long posterior lateral spinnerets, such as agelenids and hersiliids (Peters 1967). They probably facilitate both the production of sheets of fine lines, rather than of cables of lines, and the placement of these swaths of lines using movements of the highly mobile spinnerets (Fig. 3). Sheets rather than cables are useful to these spiders, which line their retreats with sheets of silk, build sheet webs to capture prey and wrap their prey in wide bands of silk (Coyle 1986; Barrantes & Eberhard 2007).

The aciniform lines of both mygalomorphs and araneomorph spiders adhere at least weakly both to each other and to the substrate, and SEM and light microscope images indicate that they have small amounts of liquid associated with them when they are produced (Kullmann 1975 on ctenizid and diplurid mygalomorphs; Weng et al. 2006 on an uloborid and an araneid; W. Eberhard unpublished on the araneid *A. argentata*). This stickiness of aciniform lines helps make functional sense of some aspects of spinneret morphology. Mygalomorphs are able to glue lines together and to the

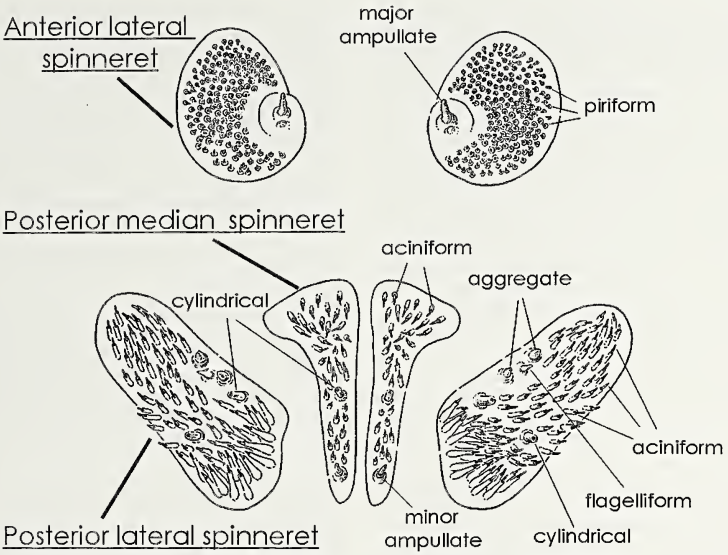

Figure 2.—Basic diagram of the locations of spigots on the spinnerets of araneoid spiders (after Coddington 1989).

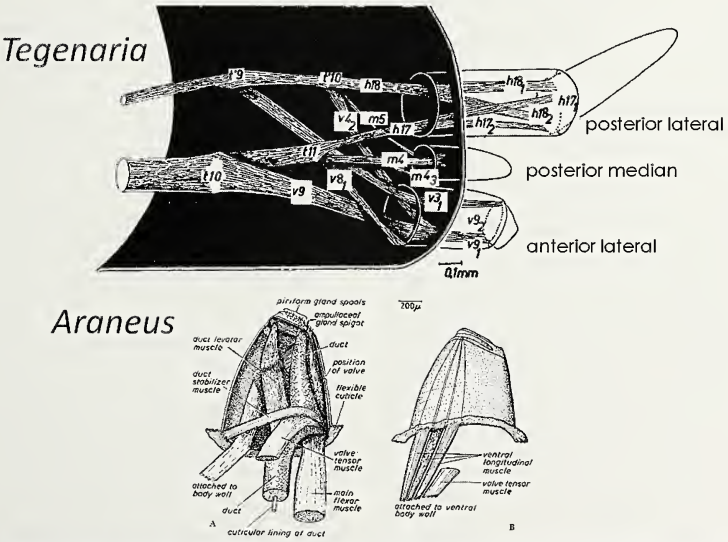

Figure 3.—The complex muscles associated with the spinnerets of an agelenid (above) and an araneid (below) indicate that these spiders are able to make diverse, finely controlled spinneret movements (above from Peters 1967; below from Wilson 1962b).

substrate, despite that fact that they lack piriform glands, whose products are used to fasten lines to other objects in araneomorph spiders (Schütt 1996; Foelix 1996; below). The aciniform spigots of araneomorphs are downstream from the piriform spigots, so their aciniform lines probably cannot be easily attached using piriform silk.

The aciniform lines also vary substantially in diameter, in both mygalomorphs (Kullmann 1975 on a diplurid; Stern & Kullmann 1981 on a ctenizid), and araneomorphs (Kullmann 1975 on an araneid; Weng et al. 2006 on an uloborid and an araneid; W. Eberhard unpubl. results on the araneid *A. argentata*). Presumably these differences are associated with the differences in aciniform spigot diameters seen in many species (Griswold et al. 2005), but nothing appears to be known regarding the possible functional significance of these differences, or the possibility that silk composition varies in lines with different diameters. In *Uloborus* there are two kinds of cells in all aciniform glands (Kovoor 1977).

Piriform gland spigots: Small masses ("attachment discs") of piriform gland products are used to attach draglines to the substrate or to other lines. They are apparently always initiated using the direct contact technique. Piriform lines are initiated either when the spider places a silk line against her spinnerets or presses her spinnerets against a substrate such as a leaf. Production of an attachment disc generally involves a short pause in spinning other lines, and in at least some cases the spinnerets rub rapidly against each other or against the substrate when an attachment is made (Schütt 1996; W. Eberhard unpubl. results on various araneid, nephilid, tetragnathid, and theridiid species). The looped forms of individual piriform lines in an attachment disc (e.g., Foelix 1996) probably result from these spinneret movements, but this behavior has never been studied in detail. Piriform lines are generally terminated almost immediately, when the spider pulls her abdomen away from contact with the substrate.

Use of the contact technique for initiation means that the piriform gland spigots do not need to be "downstream" of other spigots. In accord with this, piriform spigots consistently occur at relatively "upstream" sites, on the anterior lateral spinnerets (Fig. 2). Two additional details regarding the positions of piriform spigots on the anterior lateral spinnerets may be functionally important. The spigots are consistently at or near the tips rather than along the sides or at the bases of the spinnerets; and the surface on which the spigots are present is often relatively flat and tends to slope downward medially (e.g., Platnick et al. 1991; Agnarsson 2004; Griswold et al. 2005). Both the placement at the tip and the slanting flat field may serve to facilitate simultaneous contact between numerous piriform spigots and a flat substrate when the spinnerets are spread. Perhaps the different degrees of slant in different species (e.g., Griswold et al. 2005) are associated with different degrees to which the spinnerets are spread when producing attachment discs. The piriform spigots are also generally well placed to apply their products to the dragline emerging from the major ampullate spigots on these same spinnerets, thus allowing the spider to attach its dragline to the substrate. In some species the piriform spigots physically surround the major ampullate spigots (Fig. 2).

Microscopic examination of piriform attachment discs shows that they include liquid components, and also possibly more than one type of line (Kullmann 1975 and Stern & Kullmann 1981 on an oecobiid and an araneid; Schütt 1996 on a linyphiid and an araneid; Foelix 1996 on a thomisid). It is apparently not known whether different piriform spigots produce different products. Judging from the relatively uniform coating of apparent liquid on the piriform lines of the linyphiid *Drapestica socialis* (Sundevall 1833) (Schütt 1996), piriform lines in this species may emerge from their spigots with a liquid coating, rather than having liquid applied later. The description of Griswold et al. (2005: 59) "These spigots extrude the glue that attaches silken lines" is correct in a general sense, but does not include the thread-like products of these spigots, which are drawn from rather than "extruded" by these spigots.

The behavior of the spinnerets associated with the production of piriform silk was studied in video recordings of a large, slow-moving spider (an adult female *N. clavipes*) as she attached draglines to other non-sticky lines at the hub, and sticky spiral lines to radii. Spinneret behavior was highly stereotyped. In both types of attachment, the spider held the segment of the non-sticky line to which the attachment was to be made between her tarsi III and IV and placed it (using movements of these legs and of her abdomen) deep in the cleft between her anterior lateral spinnerets (the radius was approximately halfway down the length of her anterior lateral spinnerets). The radius often, though not always, passed over the tips of her posterior lateral spinnerets. Both the basal and the distal segments of her anterior lateral spinnerets were flexed medially, and the tips of the spinnerets rubbed rapidly back and forth against each other briefly, with one spinneret moving anteriorly while the other moved posteriorly. Probably contact occurred on the surfaces where the piriform spigots are located (Kuntner et al. 2008).

When attaching the dragline, each anterior lateral spinneret rubbed several times against the other (up to three complete cycles in about 0.77 s). Such movements may serve both to initiate piriform lines and to surround the dragline and the other line with piriform lines and glue; this could result in an increase in the surface area of these lines that is contacted by piriform products, presumably increasing the strength of the attachment that is formed.

When attaching the sticky spiral, the spider made only a single forward-backward rubbing movement with each spinneret (lasting about 0.06–0.09 s). Her posterior lateral spinnerets, which bear the spigots for the sticky spiral line and the glue that covers it, were flexed forward. This flexion occurred 0.03–0.06 s before the radius was brought into contact with her spinnerets and was maintained while the anterior lateral spinnerets rubbed against each other. Meanwhile her leg iIV pushed the sticky line ventrally and somewhat anteriorly, and the line appeared to make contact with the anterior lateral spinnerets during their rubbing movements. The anterior movements of the posterior lateral spinnerets, in combination with the fact that the spider pushed the new sticky line ventrally and anteriorly with one of her legs IV, thus brought the sticky line far enough forward that the piriform spigots were able to apply their silk to it during the rubbing movements. Finally the anterior lateral spinnerets spread apart and (often about 0.03 s later) the posterior lateral spinnerets spread and moved posteriorly as the spider pulled

her abdomen away from the radius, leaving the finished attachment.

It is possible that these piriform products differ from others, because there are other data which suggest that the attachments of sticky spiral lines to radii in araneoid orbs may not be made from "typical" piriform gland products (Kullmann 1975 on differences in silk morphology in SEM images; Eberhard 1976 on differences in physical properties; Tillinghast et al. 1981 on differences in chemical properties).

Cribellum gland spigots: A second type of line that is also both initiated and then pulled by an external agent is cribellum silk; multiple fibers are pulled from the cribellum with brushing movements of the comb of setae (the calamistrum) on the spider's leg IV. There is no need for the spigots of lines that are pulled by the spider's legs to be downstream of other spigots, and the cribellum is indeed upstream of all other spigots. In addition, the spinnerets on which cribellum spigots occur (the anterior medians) have been modified to form flat plates whose angles can apparently be modified by special muscles (Peters 1967), a design that is appropriate to allow the linear calamistrum to snag lines from the entire array with a single pass.

Pseudoflagelliform gland spigots: The placement of the spigots of the pseudoflagelliform glands is also functionally logical. These glands are thought to produce the straight baselines associated with the mat of cribellum lines in the sticky spiral of uloborids. The pseudoflagelliform spigots are on the tips of the posterior lateral spinnerets (Coddington 1987), appropriately distant from the cribellum to avoid being snagged by the calamistrum (the pseudocribellar line, which is much shorter than the cribellum lines, is presumably pulled by the walking movement of the spider rather than by the combing action of the calamistrum). The sticky spiral of the uloborid *Uloborus diversus* is initiated when the spider touches her spinnerets to a radius (Eberhard 1972), so the direct contact technique may be used to initiate the pseudoflagelliform lines.

Cylindriform gland spigots: Cylindriform gland lines are used to make egg sacs. They seem to be slightly sticky when they emerge, because some lines in egg sacs are covered with liquid (Kullmann 1975 on an araneid, a mimetid and a deinopid; Stern & Kullmann 1981 on a theridiid), and they very frequently adhere at least weakly to each other, even though the spider only briefly dabs her abdomen to the egg sac during construction; the dabs are not accompanied by short pauses, as when piriform discs are produced (Kullmann 1961; Gheysens et al. 2005; Moya et al. 2010). It thus appears that piriform silk is not used to hold sticky cylindrical gland lines together; this is consistent with morphology, as the cylindrical gland spigots are downstream with respect to the piriform gland spigots (Fig. 2)

Flagelliform and aggregate gland spigots in theridiids: The upstream placement of dragline spigots probably has still another important functional consequence in theridiid spiders, which use flagelliform and aggregate gland products to wrap and subdue prey. Initiation of these wrapping lines occurs as the spider moves toward the prey (Barrantes & Eberhard 2007), and it seems very likely (though initiation has never to my knowledge been directly observed) that these wrapping lines are initiated by being attached to the emerging trail line. The downstream placement of the flagelliform and aggregate gland spigots in theridiids (on the posterior lateral spinnerets) with respect to the ampullate gland spigots (on the anterior lateral spinnerets) (Coddington 1989; Agnarsson 2004) makes dragline initiation feasible.

The silk used in the later stages of theridiid wrapping attacks tends to be dry rather than wet (Barrantes & Eberhard 2007), presumably as aciniform lines replace wet sticky lines. Initiation of these presumed aciniform lines does not involve any obvious change in the wrapping movements of the spider's legs or abdomen. The downstream position of aciniform spigots (posterior median and lateral spinnerets) with respect to major and minor ampullate spigots, and the fact that they are also downstream or parallel in position with respect to the flagelliform spigots on the basal portions of the posterior lateral spinnerets (Agnarsson 2004), also makes it feasible that the aciniform lines are initiated by being attached to either the dragline (if it is still being produced) or to the flagelliform line.

In some of the orbicularion groups that no longer spin orbs, the tightness of the physical association between the flagelliform and aggregate spigots on the posterior lateral spinnerets is less consistent (e.g., Griswold et al. 1998, Agnarsson 2004). The possible the reasons for this dissociation are not clear.

Pholcid spigots: The spinnerets of pholcids have only small numbers of spigots compared with those of araneoids (as few as 8, with a maximum of 20 – B. Huber, pers. comm.; contrast this with >1300 spigots in *Araneus diadematus* Clerck 1757– Foelix 1996), and some glands and their spigots have been difficult to homologize with those of other spiders (Kovoor 1986; Platnick et al. 1991). The enormously enlarged tip of one spigot (the spigot for gland "B" of Millot) at the tip of the anterior lateral spinneret (Platnick et al. 1991; Huber 2000) appears to produce sticky liquid that is used both in wrapping prey (Kirchner & Opderbeck 1990; Eberhard 1992), and in making the puddle of liquid that attaches lines to the substrate (Schütt 1996). This spigot lies immediately adjacent to the spigot that probably produces the dragline (major ampullate gland; gland "C" of Millot) (Kovoor 1986; Platnick et al. 1991). Pholcids resemble theridiids in rapidly initiating sticky silk production at the beginning of wrapping attacks and then later using non-viscous silk to wrap the prey (Kirchner & Opderbeck 1990; Eberhard 1992; Barrantes & Eberhard 2007). As in theridiids, there is no perceptible pause associated with initiation of sticky silk production as the spider runs to the prey and begins to wrap it. This rapid initiation of sticky wrapping silk probably occurs when spigot B material is pulled out by (or poured onto?) the dragline while the dragline is produced as the spider moves toward the prey, in much the same way that aggregate gland silk is added to flagelliform gland silk in araneids (above). In *Pholcus phalangioides* (Fuesslin 1775) the spider applies up to four lines of silk at once to the prey (Kirchner & Opderbeck 1990), so lines from at least one additional set of spigots in addition to the major ampullates must be involved, perhaps the spigots for gland A on the posterior median spinnerets (these are thought to correspond to the minor ampullate glands) (Kovoor 1986; Platnick et al. 1991). It would be feasible (though certainly not demonstrated at the moment) for the spider to use dragline initiation for these additional minor ampullate lines during the latter stages of prey wrapping by touching the A spigots on the

median posterior spinnerets to the dragline after it emerges from spigots C on the anterior lateral spinnerets.

Pholcids use small pools of what is probably this same adhesive silk from spigot B, combined with other lines (presumably from other, smaller wide-mouthed spigots on the anterior lateral spinnerets), to fasten lines to each other and to the substrate (Kirchner 1986; Schütt 1996) (e.g., the typical function of piriform glands). The positions of the B spigots at the tips of the anterior lateral spinnerets are also appropriate for this function. It seems likely that the wrapping function for these glands in pholcids was derived from the attachment function, and indeed B glands have chemical characteristics reminiscent of piriform glands (Kovoor 1986; Platnick et al. 1991). If this derivation is correct, the position of the piriform spigots adjacent to the major ampullate gland spigots may have represented a preadaptation for the subsequent use of this sticky silk for wrapping prey. Presumably one piriform spigot became oversized as the gland product became more liquid, possibly in association with its use in prey wrapping.

Fine airborne lines: The glandular origins of very fine bridge or balloon lines are not known, but the arguments made here suggests that their spigots are located downstream of the dragline spigots, and perhaps upstream of the spigots of the thicker lines that the spider apparently attaches to these fine lines while the fine lines are being produced (Eberhard 1987). Direct observations of the spinnerets of the tetragnathid *Leucauge mariana* (Taczanowski 1881) suggested that the fine airborne lines originate on the posterior median or posterior lateral spinnerets (Eberhard 1987).

DISCUSSION

Implications.—The data above show that the consistent sites at which the spigots of different glands are placed on different spinnerets have functionally reasonable "upstream-downstream" explanations. It is also possible, however, that these explanations for spigot placement are simply an example of historical constraint. It makes functional sense, for instance, that the major ampullate spigots are not downstream of others, due to their possibly central role in initiating lines from other glands. But the major ampullate spigots apparently evolved only once (Griswold et al. 2005), and the lack of variation of major ampullate spigot placement across spiders indicates that their placements in different species probably represents (at least in some senses) only a single evolutionary event. This skepticism regarding the functional interpretations proposed here must be tempered, however, by the fact that the "upstream-downstream" arguments can explain not only why these and other spigots are located where they are in the first place (clearly, spigots are not randomly scattered over the spinnerets); they can also explain why they have not moved subsequently. The possibility of evolutionary flexibility in spigot placement is demonstrated by the fact that aciniform gland spigots were apparently regained twice independently after having been lost from the posterior median spinneret in *Pimoa* (Hormiga 1994). Additional predictions derived from the arguments presented here could offer further tests. For instance, there should be a correlation between the positions and movements of the anterior lateral spinnerets when attachments are made and the site and slant of the planar field on which the piriform spigots are located.

It is also important to note that the kinds of functional arguments made here cannot yet explain some spigot placements and thus also represent possible areas of future research. I do not understand, for instance, how the calamistrum on the spider's leg IV can snag lines from the paracribellar spigots on the posterior median spinnerets of a species like *Filistata insidiatrix* (Forsskål 1775). In this species the paracribellar lines are highly curled and presumably pulled out by the brushing action of the calamistrum (Griswold et al. 2005), but the posterior median spinnerets are shorter than the anterior lateral spinnerets, thus apparently making it difficult for the calamistrum to pull lines from the paraflagelliform spigots (Griswold et al. 2005) (perhaps the spider can protrude the posterior median spinnerets?). The functional significance of the substantial differences in the forms of the calamistra of different species has also, to my knowledge, never been discussed or related to the differences in the form of the cribellum.

Many other smaller morphological details are still mysterious, such as the "T" shaped array of piriform spigots on the anterior lateral spinnerets of *Mecynogea lemniscata* (Walckenaer 1842) and *Cyrtophora citricola* (Forsskål 1775) (Coddington 1987), the nearly complete loss of piriform spigots in immature but not adult *Eriauchenius* (=*Archaea*) *workmani* O. Pickard-Cambridge 1881 (Griswold et al. 2005), and the loss and subsequent independent recovery of aciniform spigots on the posterior median spinnerets of some species of *Pimoa* (Hormiga 1994). It is not clear why there is variability in the tightness of the physical association between the flagelliform and aggregate spigots in some orbicularions that have lost orb webs (e.g., Agnarsson 2004). The function of the "small gland" spigots on the anterior lateral spinnerets of pholcids (Kovoor 1986), which were presumed by Platnick et al. (1991) and in the discussion above to represent piriform spigots that are used to fasten lines to the substrate and other lines, needs to be confirmed. The origin of the screw lines (Kirchner & Opderbeck 1990) in pholcid webs is apparently unknown.

Future directions.—The focus here has been on morphology, but understanding the functional significance of morphology depends on combining it with behavioral data. The behavioral capabilities of spider spinnerets, however, are as yet nearly completely unstudied. The spinnerets of many species are relatively short and thus difficult to observe, but they are segmented, and are equipped with well-developed musculature (Fig. 3), suggesting that they may be capable of substantial subtlety in their movements. The observations of *Nephila* described above document brisk, highly coordinated spinneret movements. Some mygalomorph and labidognath spiders can move at least their posterior lateral spinnerets with certain dexterity, including asymmetrically raising one and lowering the other during prey wrapping) (Barrantes & Eberhard 2007). Foelix (1996) mentions lifting, lowering, twisting and spreading movements (species not specified). Perhaps, even though the context is somewhat artificial, study of spinneret movements during forcible silking can help establish the behavioral capabilities of spinnerets. Craig (2003) stated (though with no evidence) that spinneret movements have

played an important role in giving spiders great flexibility with respect to the types and character of the threads they spin.

Perhaps further study of spinneret movements will help to resolve some of these problems. Do spinnerets actually "clap" together medially to initiate airborne lines, as proposed by Blackwall (in McCook 1889), Nielsen (1931) and Eberhard (1987)? Are such claps always symmetrical (as appeared to be the case in *N. clavipes*), or is it possible for the piriform field of one anterior lateral spinneret to move medially to press on the lower interior face of the other anterior lateral spinneret and thus press on the line emerging from the major ampullate spigot? When spiders evolved to attach their draglines to other lines with piriform discs, their anterior lateral spinnerets may have already been capable of opposable movements that permitted them to "grasp" the other line to which the attachment was to be made, and thus apply piriform silk precisely to the other line. Perhaps araneomorphs evolved their relatively shorter spinnerets in association with the evolution of more types of silk glands, due to the advantage of having the spigots of different glands close to each other to facilitate coordination of production of different types of lines (B. Huber, pers. comm.).

It will be important in future work to keep in mind that the spinneret positions in taxonomic papers are somewhat unnatural, because taxonomists routinely spread the spinnerets to make the locations of different spigots easier to observe (Coddington 1989). In general, the spigots on different spinnerets are probably closer together in life than would be suggested by figures in taxonomic works. In attempting to think about "upstream – downstream" positions, it is also necessary to take into account cases in which the spider uses her leg to push a line anteriorly, as in sticky spiral production by *N. clavipes*. It will also be important to avoid typology, and keep in mind the possible consequences for spinneret use of variations in behavior; for instance, the different ways the spider grasps lines to which they are going to attach in the theridiids. *Achaearanea tesselata* (Keyserling 1884) (Jörger & Eberhard 2006) and *Tidarren sisyphoides* (Walckenaer 1842) (Madrigal-Brenes & Barrantes 2009) seem likely to affect how their spinnerets contact these lines.

Another topic that needs further work and that may provide understanding of spigot placement concerns the mechanisms that spiders use to *terminate* lines. Piriform initiation and termination is sometimes repeated literally hundreds of times very rapidly during the construction of a single orb. For instance, one mature female *M. duodecimspinosa* made 832 attachments of her hub spiral and temporary spiral to radii in the space of 428 s, or an average of 1.9 attachments/s; the time during which the spider's spinnerets were in contact with web lines (and thus the time during which piriform silk could be deposited at each attachment) was on the order of one or two tenths of a second/attachment. In other words, *M. duodecimspinosa* turns on pyriform silk production for only about a tenth of a second about twice a second, making hundreds of attachments in rapid succession. This is truly an impressive feat of coordination!

What little is known concerning termination of silk lines suggests (at least in the ampullate glands, which have long ducts) that termination generally occurs when there is a lack of liquid silk in the duct leading to the spigot, and the line breaks there as it is being pulled (Wilson 1962b; Work 1977). Presumably liquid silk then needs to be pushed to the tip of the spigot for the line to be reinitiated. It is not clear whether this termination mechanism also occurs in other glands such as the piriform and aciniform glands, which have much shorter ducts. So little is known at present that it is desirable to keep an open mind regarding whether spigot placement is also functionally related to termination.

Spigot placement could also possibly influence the spider's ability to clean its spinnerets after lines are terminated. For instance, when an adult female *N. clavipes* finishes wrapping a prey, she often "scrubs" her spinnerets together, scrapes their surfaces with the tarsus of her leg IV and then pulls the tarsus away, sometimes repeatedly.

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Eukoenenia (Palpigradi: Eukoeneniidae) in Brazilian caves with the first troglobiotic palpigrade from South America

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Abstract. Reports of Palpigradi from South American caves are rare, and no troglobiotic species have yet been described. This apparent deficiency, however, reflects merely a lack of reporting. Ten years of biospeleological surveys of 603 caves in 16 of the 26 Brazilian states, in bedrocks including limestone, quartzite, iron ore, granite, and gneiss, have led to the capture of 494 palpigrades, and specimens with troglomorphic characteristics have been found in Minas Gerais, Bahia, and Espirito Santo. Palpigrades have been found to be relatively more common in iron ore caves, and troglomorphic species apparently occupy cave habitats different from those occupied by edaphomorphic species. The description of the first troglobite species from South America is presented here. *Eukoenenia maquinensis*, new species, collected in the Maquiné Cave Minas Gerais, Brazil, has six blades in the lateral organs, seven pairs of setae on the propeltidium, six setae on the basitarsus IV (a single proximal sternal seta) and a singular chaetotaxy of opisthosomal sternites.

Keywords: *Eukoenenia maquinensis*, Neotropics, troglomorphic

The order Palpigradi Thorell 1888 includes small arachnids found in soil, leaf litter, caves, and semi-aquatic interstitial environments (Barranco & Harvey 2008). Since their original discovery in Catania (Grassi and Calundruccio 1885), researchers have found palpigrades in many locations around the world, including northern Africa, Europe, Madagascar, Australia, southeastern Asia, and both North and South America (e.g., Condé 1956, 1974b, 1984a, 1987, 1996; Peyerimhoff 1902; Harvey 2003).

In South America, only nine palpigrade species are known: *Prokoenenia chilensis* (Hansen 1901), *Eukoenenia* cf. *grassii* (Hansen 1901), and a member of the *E. mirabilis-berlesei* complex from Chile; *Eukoenenia florenciae* (Rucker 1903) from Paraguay, Colombia and Argentina; *E. grassii*, from Paraguay; *E. improvisa* Condé 1979, *Allokoenenia afra* Silvestri 1913 and *Koeneniodes notabilis* Silvestri 1913 from French Guiana; *E. janetscheki* Condé 1993 and *E. roquettei* (Mello- Leitão & Arlé 1935) from Brazil (Condé 1979, 1984a, 1986, 1993, 1996; Mello-Leitão & Arlé 1935).

Except for *Leptokoenenia* Condé 1965 (with two marine interstitial species) and *Triadokoenenia* Condé 1991 (monotypic, associated with rain forests of northeastern Madagascar), all genera of the order have species endemic to caves. However, species of the genus *Eukoenenia* Börner 1901 are by far the most highly morphologically modified and most numerous in the underground environment. Of the 66 species of palpigrades included in this genus, 27 are restricted to caves (21 in Europe, one in Cuba, and at least five in tropical Asia) (Condé 1996).

The species *E. orghidani* Condé & Juberthie 1981, found in the Bellamar cave in Cuba, is the only recognized troglobiotic species of the order Palpigradi to have been discovered in the Americas (Condé 1996), and no records of troglobiotic palpigrades have been reported from South America.

In the present paper, a new troglobiotic species of the genus *Eukoenenia*, the first from South America, is described, and various aspects related to the geographical distribution of the genus *Eukoenenia* in Brazilian caves are noted.

METHODS

Various inventories of cave fauna using the methodology proposed by Ferreira (2004) have been compiled in 603 Brazilian caves over the past ten years, including caves in 16 of the 26 Brazilian states (Minas Gerais, Goiás, Espírito Santo, Bahia, Rio de Janeiro, Mato Grosso, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul, Sergipe, Ceará, Rio Grande do Norte, Alagoas, Pernambuco and Tocantins). Caves in various lithologies were included in the inventories: carbonate rocks (limestone, dolomite, calcarenite, marble, and calcoschist), conglomerates, iron ore (hematite and itabirite), siliclastic rocks (quartzite and sandstone), and magmatic rocks (gneiss and granite).

In all the caves we conducted a thorough search for palpigrades in all potential microhabitats: on the floor of the cave, on the speleothems, and under rocks, from regions near the entrance to those deeper inside the cave. They were caught with fine brushes and fixed in 70% alcohol. The area outside the caves was also inspected when the environmental conditions appeared to be favorable for the occurrence of palpigrades. The specimens examined for this study are lodged in the Coleção de Invertebrados Subterrâneos do Laboratório de Ecologia Subterrânea do Departamento de Biologia da Universidade Federal de Lavras (UFLA), Lavras, MG, Brazil, and the Instituto Butantan, São Paulo, SP, Brazil (IBSP).

A chi-square test was used to evaluate the abundance of palpigrades in different lithologies. In order to obtain the local average yield of non-quantitative palpigrade sampling (by municipality), the total number of palpigrades collected in the caves of a municipality was divided by the number of palpigrade-inhabited caves.

The material was examined by clearing in Nesbit's solution and mounted in Hoyer's medium on 7.6 × 2.5 cm glass slides using standard procedures for mites (Krantz & Walter 2009). We made drawings under phase contrast microscopy, with measurements reported in micrometers (μm). Body length was

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Table 1.—Brazilian municipalities with occurrence of underground palpigrades.

Municipality	Caves	State	Lithology	Total abundance	Relative abundance
Iuiú	2	BA	Limestone	2	1
São Desidério	1	BA	Limestone	3	3
Itaetê	1	BA	Limestone	2	2
Afonso Cláudio	1	ES	Gneiss	2	2
Arcos	11	MG	Limestone	13	1.18
Bambuí	1	MG	Limestone	1	1
Brejo da Madre de Deus	1	PE	Granite	1	1
Corsdisburgo	1	MG	Limestone	7	7
Doresópolis	10	MG	Limestone	10	1
Felipe Guerra	2	RN	Limestone	7	3.5
Iguatama	2	MG	Limestone	6	3
Itabirito	5	MG	Iron ore	17	3.4
Itumirim	1	MG	Limestone	1	1
Lagoa da Prata	7	MG	Limestone	20	2.85
Lagoa Santa	1	MG	Limestone	7	7
Lima Duarte	3	MG	Quartzite	7	2.33
Mambaí	1	GO	Limestone	1	1
Moeda	4	MG	Iron ore	140	35
Nova Lima	10	MG	Iron ore	77	7.7
Padre Paraíso	1	MG	Granite	2	2
Pains	36	MG	Limestone	65	1.8
Paracatu	1	MG	Limestone	1	1
Prudente de Morais	3	MG	Limestone	3	1
Santa Tereza	1	ES	Granite	3	3
Sete Lagoas	1	MG	Limestone	3	3
Vargem Alta	1	ES	Marble	1	1
Varre e Sai	1	RJ	Granite	5	5
Curvelo	1	MG	Limestone	1	1
Januária/Itacarambi	1	MG	Limestone	1	1
Vazante	3	MG	Dolomite	21	7

measured from the apex of the propeltidium to the posterior margin of the opisthosoma.

The following abbreviations were used, based on Barranco & Mayoral (2007): L, total length of body (without flagellum); B, length of dorsal shield; P, pedipalpus; I and IV, legs I and IV; ti, tibia; bta1, basitarsus 1; bta2, basitarsus 2; bta3, basitarsus 3; bta4, basitarsus 4; ta1, tarsus 1; ta2, tarsus 2; ta3, tarsus 3; a, width of basitarsus IV at level of seta r; er, distance between base of basitarsus IV and insertion of seta r; grt, length of tergal seta; gla, length of lateral seta; r, length of stiff seta; t/r, ratio between length of basitarsus IV and stiff seta length; t/er, ratio between length of basitarsus IV and distance to insertion of stiff seta; gla/grt, ratio between lengths of lateral and tergal setae; B/bta, relation between lengths of prosomal shield and basitarsus IV; bta/ti, ratio between lengths of basitarsus IV and tibia IV; F, flagellar segments. Setal nomenclature follows that of Condé (1974a, 1974b, 1981, 1984a, 1988, 1989, 1992, 1993, 1994).

RESULTS

Distribution of species of genus *Eukoenenia* in Brazilian caves.—Individuals of the order Palpigradi were found in 131 of the 603 caves surveyed (21.7% of the total). We discovered these palpigrades in various municipalities in the states of Minas Gerais, Goiás, Espírito Santo, Rio de Janeiro, Pernambuco, Rio Grande do Norte, and Bahia. The lithologies of the caves in which palpigrades were found included carbonate rocks (limestone), iron ore, magmatic rocks (granite and gneiss), and siliclastic rocks (quartzite) (Table 1). Palpigrades were especially prevalent in iron ore caves, and a chi-square test showed that the abundance of palpigrades varied as a function of host rock type, with the number found in iron ore caves double the number that would have been expected.

A total of 494 individuals was found in the various habitats inside the different caves, normally under rocks or in the soil on the floor of the cave; rarely, they were discovered crawling along the walls or on speleothems. The average number of palpigrades per cave per municipality shows that these invertebrates are most abundant in the state of Minas Gerais, especially in caves in iron ore, although many are also found in limestone caves (Fig. 1).

In the epigean environment in the vicinity of the caves, we only found palpigrades in the state of Minas Gerais (municipalities of Iguatama, Lavras, Pedro Leopoldo, Novo Oriente de Minas, Arcos, and Pains). They were especially prevalent in the latter two municipalities, where dozens of individuals were found under the rocks in the forest; however, all sightings were made during rainy periods. It seems probable that during the dry seasons they penetrate the interstices of the soil to protect themselves from the dry conditions of the surface.

All exemplars collected in Brazilian caves were identified as *Eukoenenia*. In addition to the troglobiotic species found in the Maquiné cave, described in this study, individuals collected in six other caves in the states of Espírito Santo, Minas

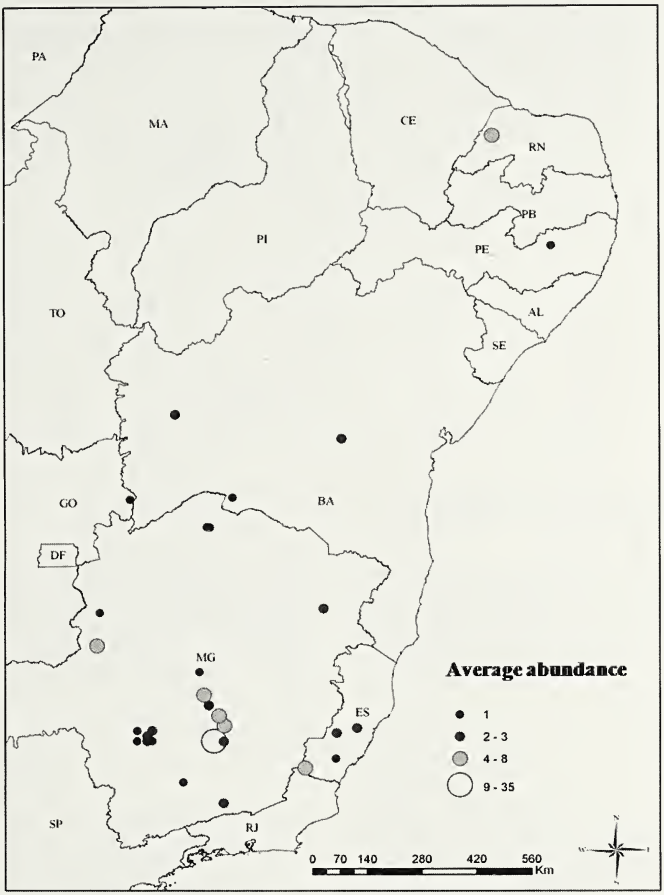
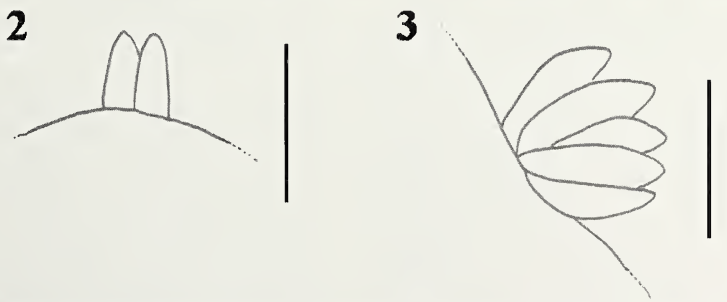


Figure 1.—Distribution of the municipalities with occurrence of subterranean palpigrades in Brazil and its respective average abundances.

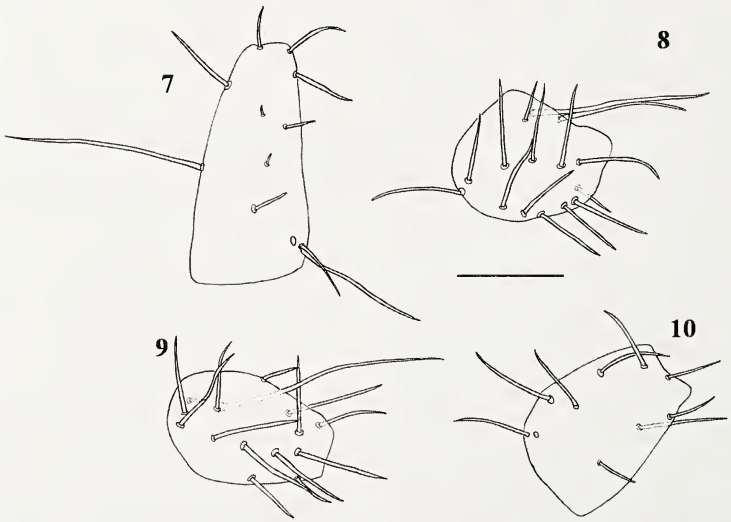


Figures 2, 3.—*Eukoenenia maquinensis* new species (holotype): 2. Frontal organ, dorsal view; 3. Lateral organ, dorsal view. Scale bars: 32.5 µm.

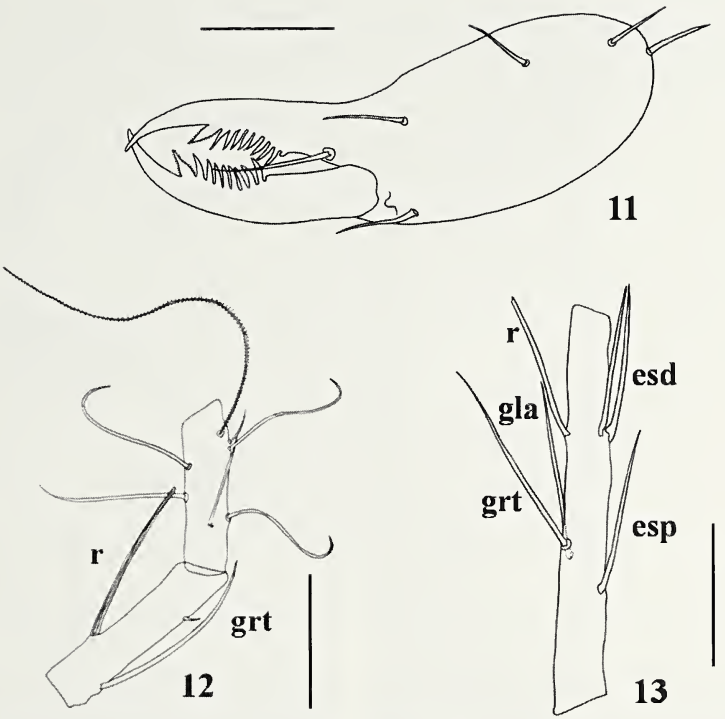
Figures 4–6.—*Eukoenenia maquinensis* new species (holotype): 4. Propeltidial chaetotaxy; 5. Metapeltidial setae; 6. Deuto-tritosternal setae. Scale bars: 150 μm (Fig. 4), 100 μm (Fig. 5), 50 μm (Fig. 6).

Gerais and Bahia presented troglomorphic traits, such as lengthening of appendices and the flagellar segments and an increase in body size. These other troglomorphic species are under description. The study of the edaphomorphic species captured has revealed the presence of at least four undescribed species.

We observed these troglomorphic species moving along the walls and speleothems, whereas the edaphomorphic species were generally hidden under rocks in the soil on the cave floor, although two were found walking on top of water accumulated in travertine dams in the Lapa Nova cave in Vazante and



Figures 7–10.—*Eukoenenia maquinensis* new species (paratype): 7. Coxa I; 8. Coxa II; 9. Coxa III; 10. Coxa IV. Scale bar: 100 μm.



Figures 11–13.—*Eukoenenia maquinensis* new species (holotype): 11. Chelicerae; 12. Basitarsus 3–4 of leg I; 13. Basitarsus IV. Scale bar: 100 μm.

another in the cave of Santuário in Pains, all in the state of Minas Gerais.

TAXONOMY

Family Eukoeneniidae Petrunkevitch 1955
Genus *Eukoenenia* Börner 1901

Koenenia Grassi & Calandruccio 1885:165 [junior primary homonym of *Koenenia* Beushausen 1884 (Mollusca: Bivalvia)].

Koenenia (*Eukoenenia*) Börner 1901:551.

Type species.—*Koenenia mirabilis* Grassi & Calandruccio 1885, by monotypy.

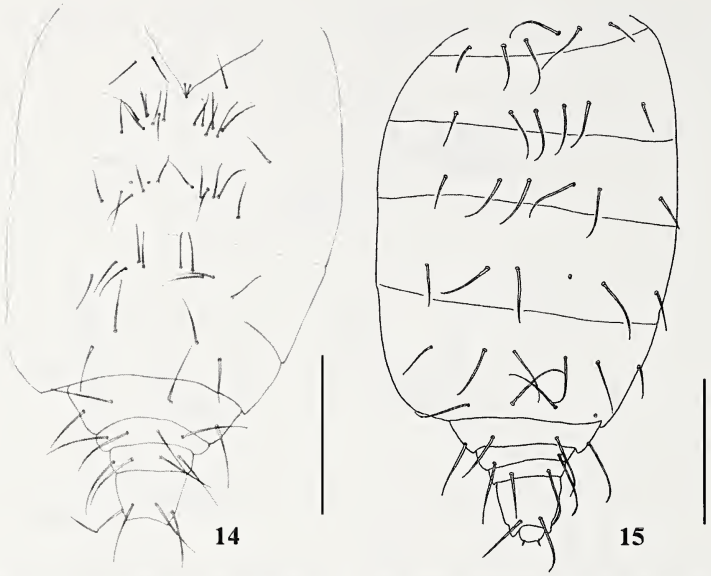
Eukoenenia maquinensis new species
(Figs. 2–20)

Material examined.—Brazil: *Minas Gerais*: Holotype adult female, Maquiné cave (collected from a speleothem), Cordisburgo (19°11′15″S, 44°18′45″W), 16 December 2007, R.L. Ferreira (IBSP, IBSP05). Paratype: 1 adult female, Maquiné cave, Cordisburgo (19°11′15″S, 44°18′45″W), 16 December 2007, R. L. Ferreira (UFLA, ISLA 502).

Diagnosis.—*Eukoenenia maquinensis* differs from all other species of the genus by the following combination of characters: presence of 6 blades on prosomal lateral organs; propeltidium with 7 + 7 setae; six setae on basitarsus IV with a single proximal sternal seta; opisthosomal sternites IV–VI with 14, 13, and 11 setae, respectively, in an irregular row.

Description.—*Prosoma.* Frontal organ with two branches, blunt apically, each 5.5 times longer than wide (55 μm/10 μm) (Fig. 2). Lateral organ with six pointed blades, each 6.7 times longer than wide (33.75 μm/5 μm) (Fig. 3); Fig. 3 only shows five blades due to the hidden position of the sixth blade. Propeltidium with 7 + 7 short setae, first pair on either side of frontal organ longer than others (Fig. 4). Metapeltidium with 3 + 3 setae (t_1, t_2, t_3), each of a different length; outer setae shortest (157.5 μm, 125 μm and 115 μm) (Fig. 5). Deutotritosternum with nine or eight setae in U-shaped arrangement (Fig. 6). Chaetotaxy of coxae I–IV: 11, 15, 15 and 9 (Figs. 7–10). The holes in Figures 7 and 10 represent the insertions of each of the respective setae, which are positioned just near each hole.

Chelicerae with 9 teeth on each finger; 4 dorsal setae and 1 ventral seta inserted near the third segment, and 1 seta inserted near the row of teeth of the second segment (Fig. 11).



Figures 14, 15.—*Eukoenenia maquinensis* new species (holotype): 14. Opisthosoma, dorsal view; 15. Opisthosoma, ventral view. Scale bar: 300 μm.

Basitarsus 3 of leg I slender, 4.23 times longer than wide, with 3 setae (*grt* 140 μm; *r* 125 μm). Seta r shorter than segment (137.5 μm/125 μm, *t/r* = 1.1), inserted in proximal half and surpassing hind edge (42.5 μm/125 μm, *s/er* = 0.34) (Fig. 12). Basitarsus of leg IV long, 9.1 times longer than wide, with 6 setae (2 *esd*, *esp*, *gla*, *grt* and *r*) (Fig. 13), bta/ti 1.07. Stiff seta r 2.75 times shorter than tergal edge of article (275 μm/100 μm, *t/r* = 2.75) and inserted in distal third (275/185, *t/er* = 1.48). Seta *esp* proximally inserted, followed by *grt* and *gla*, more or less at the same level, all of them in proximal half.

Opisthosoma: Tergites II–VI with 3 + 3 setae each, 2 pairs of tergal setae (t) (t_1, t_3) between both slender setae (s). Tergites VII–VIII with 2 + 2 setae, only t setae present and without s (Fig. 14). Sternite III with 2 + 2 setae. One seta on left side of this structure was not represented in the drawing, but was visible unattached near the sternite. Its insertion was not represented due to the difficulty in finding it precisely. Sternites IV–VI with 14, 13 and 11 setae in slightly irregular transverse row, all of them of similar shape and with length varying between 65–75 μm, 52.5–77.5 μm and 72.5–82.5 μm respectively. Sternites IV–V each with two glandular pores. Sternites VII–VIII with 2 + 2 setae. Segments IX–XI each with 6 setae (Fig. 15).

Genitalia: With 2 lobes, first lobe (Fig. 16) with 11 + 12 setae in 5 transverse rows, 4 sternal 2 + 2, 2 + 3 (asymmetry caused by dislocations due to the lack of regular and/or the presence of additional setae), 2 + 2, 1 + 1 and distal 4 + 4, of which a_1, a_2, a_3, a_4 measure 35 μm, 30 μm, 37,5 μm and 50 μm, respectively. Second lobe (Fig. 17) with 3 + 3 setae (seta y was possibly lost during the collection or the specimen presents an asymmetry) (x, y, z), measuring 32.5 μm, 40 μm, and 30 μm, respectively; six glandular orifices. Spermathecae triangular, with the base measuring 15 μm and the height measuring 10 μm.

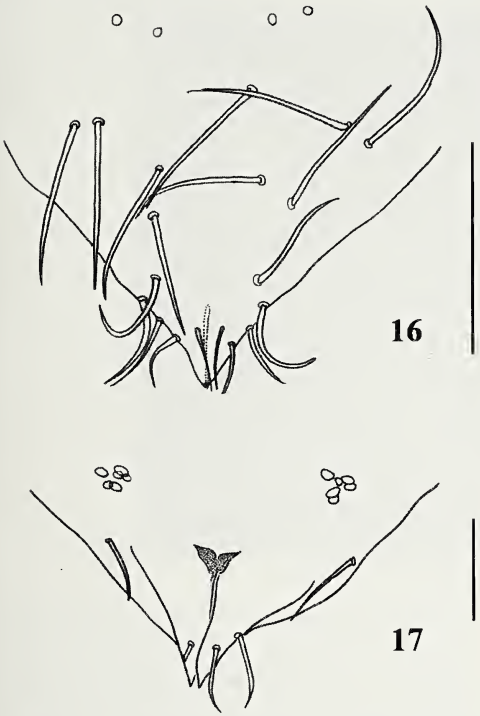
Flagellum: Longer than opisthosoma, with 14 long, slender articles (Fig. 18). First, thirteenth and fourteenth segments considerably shorter than others. First 3 segments have structures similar to a crown of spines around the extremity, with 11 long setae inserted in the distal half. Fourth, sixth and eighth segments without the crown of spines and with 9 long setae inserted in distal third. Fifth, seventh and ninth segments also with spines on their extremities and with 8 long setae inserted in distal half (Fig. 19). In the other segments, the crown of spines is lacking. Tenth segment with 9 long setae inserted in the distal half. Eleventh segment with 8 long setae in proximal half. Twelfth and thirteenth segments with 8 long setae inserted in proximal third. Last segment with 6 long setae inserted in middle of segment and 4 setae inserted apically (Fig. 20).

Dimensions (μm): See Table 2.

Habitus: See Fig. 21

Etymology.—The specific name refers to the cave, Maquiné, where the specimens were found.

Habitat.—Maquiné cave is the only known habitat of *E. maquinensis*. This cave is the oldest tourist cave in Brazil and has been exploited for this purpose since 1908. In 1967, the infrastructure was modernized to include not only stairs and



Figures 16, 17.—*Eukoenenia maquinensis* new species (holotype): 16. Female genitalia, first lobe; 17. Female genitalia, second lobe. Scale bars: 100 μm (Fig. 16), 50 μm (Fig. 17).

topographical alterations to the floor of the cave, but also electric lights. At the far end of the cave, the relative humidity is approximately 91%, and the average temperature is about 24° C. The trophic resources consist of organic material left during the installation of the tourist infrastructure, such as wood scraps, as well as scraps of food left by tourists during their visit to the cave and small plants growing near the lights. The specimens described here were collected in an area not subjected to visitation by tourists.

DISCUSSION

The environments suitable for populations of palpigrades include caves and other subterranean environments, and these invertebrates have been reported from such systems in many locations around the world, including Europe, Asia, Central America and Africa (e.g., Condé 1984a, 1987, 1996; Barranco & Harvey 2008).

Caves in sixteen of the Brazilian states were surveyed, and palpigrades were found in seven of these states. Moreover, since relatively few surveys of cave fauna have been conducted in the country, the geographical distribution of the palpigrades in Brazilian caves is probably much greater than that described here. Furthermore, some regions had been poorly studied, as the Central Amazon, where studies revealed a high abundance of a single species, *E. janetscheki* (Condé 1993; Adis et al. 1997).

Biological surveys of some 350 caves in Brazil have been previously reported in the literature (Pinto-da- Rocha 1995; Trajano 1996, 2000; Gomes et al. 2000; Zeppelini Filho et al. 2003; Prous et al. 2004; Ferreira 2005; Silva 2006). In these papers, few palpigrades have been reported, except for iron ore caves (Ferreira 2005). The reports of Trajano (1996, 2007) for the caves of Olhos DÁgua (MG) and the System of Areias (SP) include no taxonomic identification. Moreover, this author gave little emphasis to these arachnids, failing to include information about abundance and microhabitat, as well as the behavior of individuals prior to collection. This

Table 2.—Measurements (μm) of selected body parts of the two type specimens of *Eukoenenia maquinensis*.

Body part	Female (Holotype)	Female (Paratype)
L	1490	2140
B	435	462.5
Pti	235	252.5
PBta1	90	95
PBta2	105	112.5
Pta1	55	60
Pta2	75	75
Pta3	80	112.5
Iti	320	320
IBta1+2	245	260
IBta3	137.5	147.5
IBta4	115	112.5
Ita1	70	70
Ita2	80	72.5
Ita3	215	220
IVTi	255	252.5
IVBta	275	270
IVTa1	102.5	100
IVTa2	125	130
A	30	25
Er	185	187.5
Grt	137.5	130
Gla	127.5	135
R	100	100
t/r	2.75	2.7
t/er	1.48	1.44
Gla/grt	0.92	1.03
B/bta	1.58	1.7
Bta/ti	1.078	1.07
Flagelo	3865	-
FI	197.5	-
FII	240	-
FIII	275	300
FIV	290	325
FV	250	-
FVI	320	305
FVII	265	275
FVIII	332.5	325
FIX	260	260
FX	377.5	385
FXI	372.5	375
FXII	352.5	320
FXIII	170	330
FXIV	162.5	175

Figures 18–20.—*Eukoenenia maquinensis* new species (holotype): 18. First six flagellar segments; 19. Fifth flagellar segment; 20. Fourteenth flagellar segment. Scale bars: 600 μm (Fig. 18), 100 μm (Fig. 19), 150 μm (Fig. 20).

lack of information, in conjunction with the limited number of records of palpigrades, has limited our understanding of their behavior and ecology. Moreover, inadequate collection methods in caves may have led to the misconception that palpigrades are rare in underground Brazilian systems. As shown in this paper, more than 20% of the caves surveyed have palpigrades, which shows that these organisms are not rare in Brazilian caves.

Palpigrades have been discovered in epigean environments near cave entrances, as well as in their disphotic hypogean interiors, a fact that probably reflects the high humidity prevailing when collections were made. These populations can stay inside and outside of caves in the same territory.

Condé (1996) affirms that the most likely places to find palpigrades inside caves are spaces under rocks, in the soil on the floor of the cave, or moving around on the ground or walls. He explains that the occupation of these different habitats is determined by factors such as the hygrometry and the movement of air in the cave. During the collecting process, we observed that the troglomorphic palpigrades were frequently found walking along the walls and on speleothems, whereas the edaphomorphic species were found only under rocks or in the soil. Similar information is reported for troglomorphic individuals of *E. orghidani* (in Cuba) and *E. spelaea* (in the Alps of Provence) found walking around exposed on stalagmites (Condé 1984b). The adoption of this exposed habitat may reflect behavioral modifications that have accompanied the morphological adaptations linked to the underground environment. Therefore, the occupation of habitats unlike those inhabited by palpigrades under other circumstances seems to be related both to environmental aspects of the cave in which they are found and to the degree of specialization of the species in the underground environment.

The greater frequency of palpigrades in iron ore caves may be explained by the structural and functional characteristics of this type of underground system. These rock systems, especially the weathered mantle ("canga") covering the mother rock, include numerous minute conduits forming a network of interstitial spaces (meso- and microcaves) which are linked to the larger caverns, thus facilitating colonization of regions far from the entrance (Ferreira 2005). Furthermore, the epigean vegetation associated with iron ore is relatively sparse and provides rather limited leaf litter (Ferreira 2005), making the epigean environment unfavorable for the survival of soil fauna.

The troglomorphic species described here as *Eukoenenia maquinensis* displays various troglomorphic characteristics. These include reduction of the length and number of setae of the propeltidium (7 + 7) as in *E. naxos* Condé 1989, a reduction in the number of setae of the basitarsus of leg IV, with six setae instead of seven (absence of an esp seta), and a flagellum composed of 14 narrow and much elongated segments. The presence of tiny setae in the propeltidium is shared with other troglomorphic species as *E. gasparoi* Condé 1988 (10 + 10 setae), *E. thais* Condé 1988 (10 + 10) and *E. maros* Condé 1992 (10 + 9).

Moreover, this species has elongated appendages, such as the elongation of the basitarsus IV of *E. maquinensis*, which is longer than the tibia, with a bta/ti ratio of 1.07. This value is close to that found for *E. naxos* (bta/ti = 1.10), considered to be the species that has reached the highest level of underground evolution, with the exception of the lateral organs of the prosoma (Condé 1996). The mean value of *Blbta*

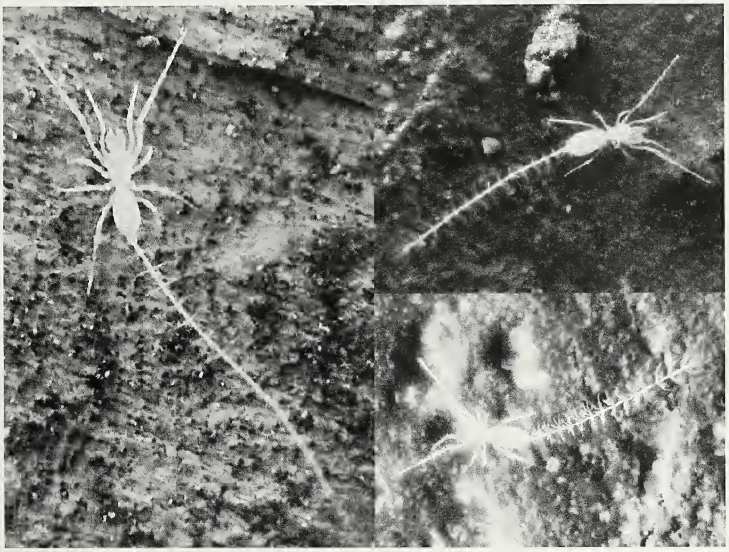


Figure 21.—Habitus of *Eukoenenia maquinensis* new species.

IV in the two specimens is 1.64, close to that of other cave species such as *E. naxos* (1.71), *E. thais* Condé 1988 (1.61), and *E. grafittii* Condé & Heurtault 1994 (1.59) (Condé 1998).

Condé (1996) considers body length to be a very arbitrary criterion for determining troglomorphism, since it is related to how stretched out an individual is in the preserving solution when measurements are taken. The holotype of *Eukoenenia maquinensis* measured only 1.49 mm, but this would correspond to approximately 2 mm, since the specimen shrank upon contact with the 70% alcohol used for preservation. The paratype preserved in 60% alcohol measured 2.14 mm, which is a more realistic representation of the adults' real size.

Furthermore, the flagellum is extremely fragile and is rarely preserved. If it survives the original capture, it seldom survives subsequent manipulation. Few specimens have been described with an intact flagellum, although Condé (1996) suggests that this length varies from 1.36 to 3.25 mm for a body length of 0.97 to 2.20 mm for adult cave species. If this is accurate, *E. maquinensis* has the longest flagellum reported for a species of *Eukoenenia*, with a length of 3.865 mm.

The lateral organs of *Eukoenenia maquinensis* are composed of six elements, similar to that of *E. spelaea* (Peyerimhoff 1902) (5–6), *E. depilata* Rémy 1960 (6), *E. remyi* Condé 1974 (4–6), *E. maroccana* Barranco & Mayoral 2007 (6) and *E. guzikae* Barranco & Harvey 2008 (6).

It was not possible to establish the deutotritosternal chaetotaxy because one of the specimens had nine setae while the other had only eight setae. The number of specimens collected was inadequate to determine if this variation in the setae represented a population characteristic or if one of the specimens served as an exception.

The holotype genitalia suggest asymmetry caused by dislocations due to the lack of regular and/or the presence of additional setae, not unusual in *Eukoenenia*. Unfortunately, the genital lobes of the paratype were damaged during slide mounting. It is impossible to determine if this asymmetry is an exclusive trait of the holotype female; in that case, the actual number of setae would be 11+11 or 12+12. In the opisthosomal sternites IV–VI the tip of the lateral setae is similar to the tip of the paramedian setae, hence, it is very difficult to distinguish the thickened setae (a) from normal setae (s).

Eukoenenia maquinensis is certainly one of the most modified palpigrades adapted to the underground environmental conditions. Many models concerning the evolution of subterranean lineages state that isolation (due to climatic changes) was more pronounced in temperate regions than in tropical areas. This would be the reason why there are so many modified troglobiotic species in temperate areas. However, the strongly modified species described here suggests that the effects of climatic changes in Neotropics (leading to isolation in subterranean habitats) could have led to the same effects observed in the temperate areas, at least for some groups such as the palpigrades.

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On the *Cryptocellus peckorum* and *Cryptocellus adisi* groups, and description of a new species of *Cryptocellus* from Brazil (Arachnida: Ricinulei)

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Abstract. A new species of Ricinulei of the genus *Cryptocellus* Westwood 1874 is described from the Madeira-Purus Interfluve, Amazonas, Brazil. It shares a set of apomorphies with *Cryptocellus peckorum* Platnick & Shadab 1977 and *Cryptocellus tarsilae* Pinto-da-Rocha & Bonaldo 2007, with which it forms an assemblage of related species herein named the *peckorum* group. A second group of species, the *Cryptocellus adisi* group, is formed by the following species: *Cryptocellus adisi* Platnick 1988, *Cryptocellus florezi* Platnick & García 2008, and *Cryptocellus lisbethae* González-Sponga 1998.

Keywords: New World, Amazon rainforest, Madeira-Purus interfluve, BR-319 highway, taxonomy, systematics

The arachnid order Ricinulei has been increasingly capturing attention of New World specialists, and over the last seven years several new species have been described: *Cryptocellus abaporu* Bonaldo & Pinto-da-Rocha 2003; *C. icamiabas* Tourinho & Azevedo 2007; *C. tarsilae* Pinto-da-Rocha & Bonaldo 2007; *C. florezi* Platnick & García 2008; *C. platnicki* Botero-Trujillo & Pérez 2008; *C. luisedieri* Botero-Trujillo & Pérez 2009 (Bonaldo & Pinto-da-Rocha 2003; Botero-Trujillo & Pérez 2008, 2009; Pinto-da-Rocha & Bonaldo 2007; Platnick & García 2008; Tourinho & Azevedo 2007); and advances undertaken in the fields of functional, structural biology, and genetics (Talarico et al. 2005, 2006).

The taxonomy and systematic foundation of New World representatives of the order Ricinulei were established by Platnick and his co-workers (e.g. Platnick & Shadab 1976, 1977, 1981; Platnick & Paz 1979; Platnick, 1980; Platnick & Pass 1982). Several new species were described from the New World, and the current generic and species-group divisions were established. The groups proposed by Platnick are stable and mostly supported by the characters of the male tarsal process. However, species of Ricinulei seem to be conservative, bearing very similar external morphology, and some species give the impression of a morphological mosaic of several different species (Tourinho & Azevedo 2007).

In this paper we describe a new species from Brazil, *Cryptocellus conori*, and propose the *Cryptocellus peckorum* group. The group includes the new species herein described and three related species previously described: *C. peckorum* Platnick & Shadab 1977; *C. tarsilae* and *C. lampeli* Cooke 1967. The four species share characters present on the accessory piece, basitarsus and teleotarsus II of leg III, cucullus and ventral abdomen. A second group of species, the *Cryptocellus adisi* group, is also defined on the basis of characters of the male tarsal process.

We also report some new records of *C. becki* Platnick & Shadab 1977 from the city of Manaus, Amazonas state. The new species was collected in a remote site in the Amazonas State in Brazil, between the rivers Madeira and Purus, one of the most important Amazonian regions for biodiversity (Py-Daniel et al. 2007) and under strong anthropogenic pressure (Fearnside 2005; Fearnside & Graça 2006).

METHODS

The specimens of *C. conori* were collected using both Winkler extractors and visual nocturnal search and are preserved in 70% ethanol. The specimens of *C. becki* were collected using Winkler extractors, and all geographical coordinates provided were obtained from the site coordinates report in the website Large Scale Biosphere Experiment in Amazonia (online at http://www.lbaeco.org/cgi-bin/web/sites/sites_report.pl). The morphological terminology follows Platnick & Shadab (1976, 1977, 1981) and Cokendolpher (2000); the general description is based on Cokendolpher (2000) and Cokendolpher & Enríquez (2004), who focused essentially on significant taxonomic structures and colors. All measurements are in mm. The specimens are lodged in the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil.

TAXONOMY

Family Ricinoididae Ewing 1929
Genus *Cryptocellus* Westwood 1874
Cryptocellus foedus Westwood 1874:201.

Type species.—*Cryptocellus foedus* Westwood 1874, by monotypy.

Cryptocellus conori new species
(Figs. 1–20)

Type material.—BRAZIL: *Amazonas*: Male holotype, 30 km Igapó -Açu, Careiro, 04°54′57″S, 61°06′45.4″W, 23 July 2007, visual nocturnal search, E.H. Wienskoski (INPA 23). Paratypes: 1 female, Careiro (Area 1, Forest 2), 04°09′55.4″S, 60°08′00.37″W, 5 July 2007, Winkler extractor (INPA 25); 1 nymph, Careiro, 04°09′26.3″S, 60°07′53″W, 6 July 2007, visual nocturnal search, E.H. Wienskoski (INPA 24).

Etymology.—A noun in apposition. In Amazonian mythology Conori was the powerful and brave queen of the female warriors "Icamiabas", related to the Amazon warriors from Capadocia and described in the chronicles of Dominican friar Gaspar de Carvajal.

Diagnosis.—*Cryptocellus conori* shares with all other species of the *peckorum* group three basic synapomorphies: fixed male

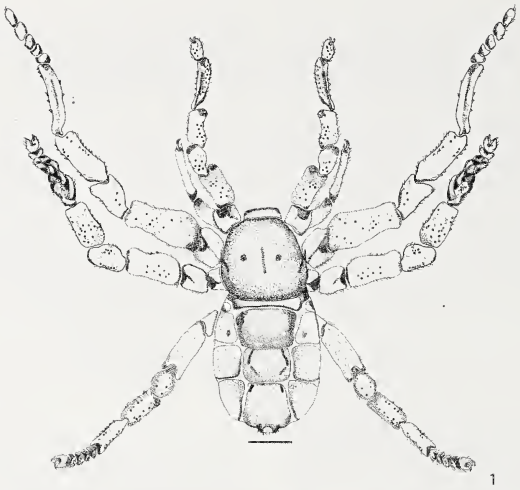
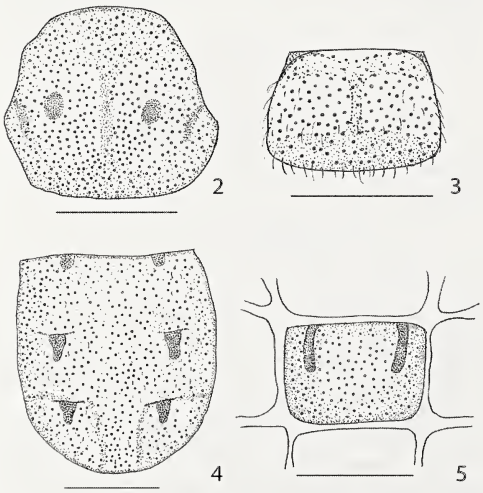


Figure 1.—*Cryptocellus conori* new species, male holotype, dorsal view. Scale bar = 1.0 mm.

accessory piece of leg III thin; both movable and fixed piece curved, and with a sinuous contour; and basitarsus of leg III moderately inflated (longer than wide). The species possess a ventral opisthosoma with three pairs of median pits containing tubercles, the anterior pair smaller than the posterior pair, those with darker and smoother tegument (Fig. 4); no abdominal pits have been reported for *C. tarsilae*, *C. peckorum* and *C. lampeli*; proximal telotarsus II distally without prolateral tubercles as in *C. peckorum*. Apex of accessory piece distally crenulated (Figs. 8, 9), inner half of spermathecae trilobate, outer half acuminate (Fig. 15), in *C. tarsilae* both inner and outer spermathecae bilobate, female of *C. lampeli* and *C. peckorum* not known.



Figures 2–5.—*Cryptocellus conori* new species, male holotype: 2. Prosoma, dorsal view; 3. Cucullus, dorsal view; 4. Opisthosoma, ventral view; 5. Tergite XI. Scale bars = 1.0 mm.

Description.—*Male holotype:* Body total length, excluding pygidium, 3.9, cucullus 0.5 long, greatest width 0.8, prosoma 1.0 long, 0.9 wide between legs II and III; opisthosoma 2.9 long, 1.9 wide near middle of tergite; legs I 3.8, II 6.8, III 5.0, IV 4.8. General body color (in 70% ethanol) dark red, intersegmental membranes orange; median and posterior portion of ventral opisthosoma lighter. Cucullus dark red, but lighter than prosoma, orange in middle. Prosoma, opisthosoma, legs and cucullus covered with numerous tubercles (Fig. 1); iridescent tubercles, showing shades of purple and dark green, present on: prosoma (Fig. 2), opisthosoma, ventral opisthosoma (Fig. 4), legs and sternal region. Prosoma dark red, much darker at lateral and posterior margin. Tergal tubercles uniformly distributed (Fig. 5). Legs and lateral margin of prosoma covered by both straight and curved whitish setae; ventral opisthosoma covered with numerous setae, concolorous with the body. Prosoma as long as wide, with numerous tubercles uniformly distributed (Fig. 2). One pair of lateral eyes, cucullus densely covered with tubercles, wider than long; anterior margin straight, posterior depressed and rounded (Fig. 3); covered with many white setae, the longest on median portion. Chelicerae: fixed finger with four teeth (distal longer than others); movable finger with 9 teeth (basal almost vestigial). Sternal region with coxa I not meeting tritosternum; coxae II, III and IV touching medially. Opisthosomal tubercles uniformly distributed. Pygidium with very slight distal dorsal notch on basal segment; no ventral notch. Pedipalps orange, with discrete tubercles. Distal leg coxae darker, leg tarsi light

Figures 6–9.—*Cryptocellus conori* new species, male holotype: 6. Male leg III, anterior view; 7. Male leg III, posterior view; 8. Acessory tarsal process, anterior view; 9. Acessory tarsal process, posterior view. Scales bar = 0.5 mm.

red. Leg formula II > III > IV > I; trochanter prolateroventral apophysis of leg III and IV absent. Apex of accessory piece distally crenulated (Figs. 8, 9), basitarsus of leg III moderately inflated (longer than wide). Legs with numerous tubercles.

Female paratype: Similar to male, except as follows. Body total length, excluding pygidium, 5.1, cucullus 0.8 long, greatest width 1.0, prosoma 1.9 long, 2.0 wide between legs II and III; opisthosoma 3.2 long; 2.7 wide near middle tergite; legs I 4.2, II 8.0, III 6.0, IV 6.1. Leg formula II > IV > III > I. Opisthosoma: abdominal tubercles absent only in paramedian portion, lighter than other regions (Fig. 14). Cucullus: rounded tubercles concentrated on median portion and posterior margin (Fig. 12). Pygidium with "V" notch on dorsal margin of basal segment. Spermathecae wide and short, inner half trilobate, outer half acuminate (Fig. 15).

Nymph paratype: Body total length, excluding pygidium 4.3, cucullus 0.5 long, greatest width 0.6, prosoma 1.3 long, 0.8 wide between legs II and III; opisthosoma 3.0 long; 2.8 wide near middle of tergite; legs I 3.1, II 5.8, III 3.6, IV 4.0. Leg formula II > IV > III > I. General body color (in 70% ethanol) orange, intersegmental membranes dark yellow (dorsal view). Ventral opisthosoma lighter than prosoma, intersegmental membranes light yellow. Cucullus, legs (femur, patella and tibia of legs I and II: orange), sternal region and pedipalps (distal segment: dark yellow) light yellow. Carapace more densely covered with tubercles than male and female, absent on anterolateral border (Fig. 17). Cucullus slightly wider than long (Fig. 18), slightly depressed in posterior margin.

Distribution.—This species is known only from the type locality (Fig. 20).

Notes on the biotope.—Specimens of *C. conori* were collected at a location in the Solimões formation (Araujo et al. 1978; Rosseti et al. 2005). Its topography is predominantly flat, with tabular interfluvials and hills with Tertiary sedimentary deposits, known as "paleo-várzea" (Mauro et al. 1978). The soil is reddish-yellow (podzolic) and the vegetation is characterized as Dense Tropical Forest (Araújo et al. 1978; Doi 1978). This region has areas of savanna-like vegetation, spotted-like mosaic field islands distributed in large areas of continuous upland forest, and this landscape pattern contrib-

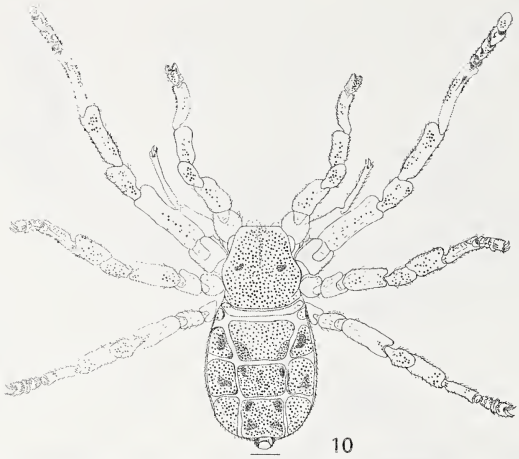
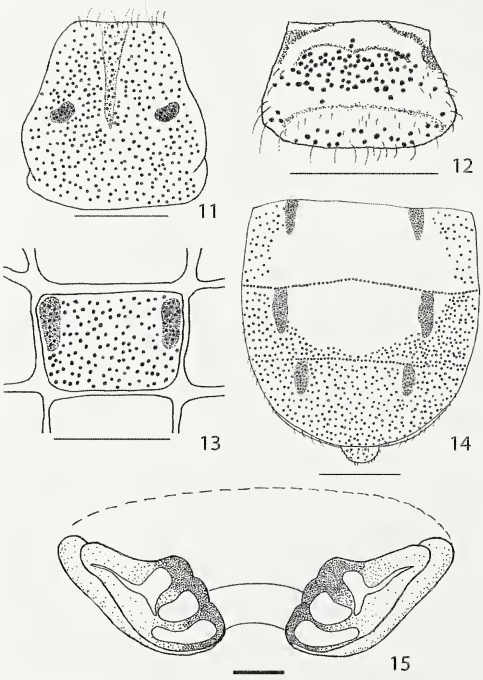


Figure 10.—*Cryptocellus conori* new species, female paratype, dorsal view. Scale bar = 1.0 mm.



Figures 11–15.—*Cryptocellus conori* new species, female paratype: 11. Prosoma dorsal view; 12. Cucullus, dorsal view; 13. Tergite XI; 14. Opisthosoma, ventral view; 15. Spermathecae, ventral view. Scales bars 11–14 = 1.0 mm; scale bar 15 = 0.5 mm.

utes directly to regional-scale diversity in the Amazon basin (Py-Daniel et al. 2007). This region is characterized by open vegetation, hosting a complex of several Amazonian natural fields, locally called "campinas", which are very numerous in this interfluvial region of the Madeira and Purus Rivers. The fields and forests host several unique species and are regarded as one of the most diverse sites in the Amazon forest (Py-Daniel et al. 2007). Several species of animals and plants were collected during these campaigns. Along with *C. conori* several new species of harvestmen and spiders are still being processed in our laboratory at Instituto Nacional de Pesquisas da Amazônia. New species of vertebrates and plants were collected on the same field trip: one new subspecies of saddleback tamarin, *Saguinus fuscicollis* Röhe, Silva-Junior, Sampaio & Raylands, 2009 (Röhe et al. 2009), a new species of palm has been diagnosed but not yet published (T. Emilio, pers. comm..), and a new species of crow, endemic to these local savanna-like spot fields in the interfluvials (M. Cohn-Haft, personal communication).

All of these species are endangered by the construction of the BR-319 highway, which is planned to connect the city of Manaus (Amazonas State) to Porto Velho (Roraima State). The highway will link the Amazonas State with the deforestation arc, the largest deforested area in the north of Brazil, including the states of Rondônia, Pará, Acre and northern Mato Grosso and Tocantins, and it would be a focus for migration and unordered human occupation, illegal occupation of lands by land grabbers, and mechanized agricultural crops of soybean and rice. These factors together will accelerate the destruction of the forest along the highway, in several sites physically distant from the road, although under its influence (Fearnside 2005; Fearnside & Graça 2006; Fearnside et al. 2009). Along with the highway there are projects to build powerful hydroelectric power plants in this interfluvial region, which will contribute heavily to the environmental damage and degradation along the interfluvials, as has already occurred

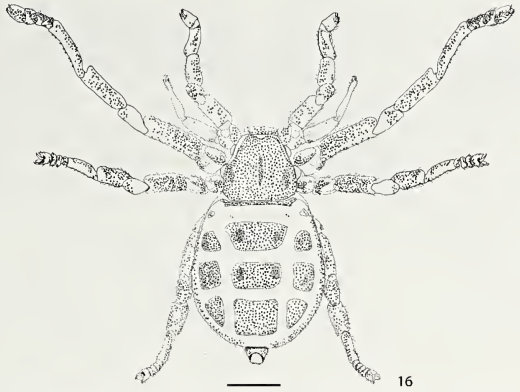


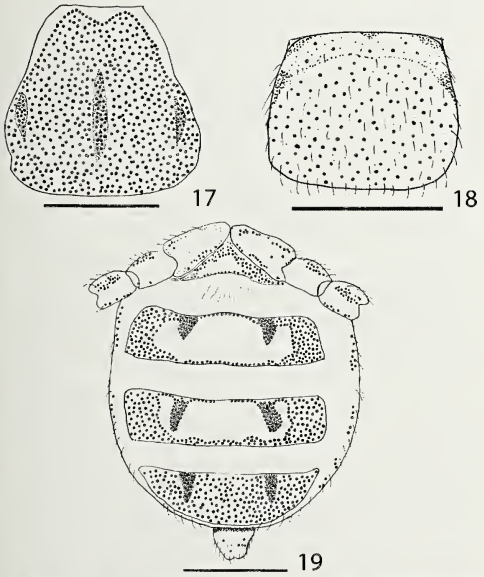
Figure 16.—*Cryptocellus conori* new species, paratype nymph, dorsal view. Scale bar = 1.0 mm.

with the lake of Balbina, and the region where the Balbina power plant was built (Fearnside 1989).

Cryptocellus becki Platnick & Shadab 1977

Cryptocellus becki Platnick & Shadab 1977:11, figs. 37–50.

Type locality.—Brazil, Amazonas, near Manaus, Reserva Ducke.



Figures 17–19.—*Cryptocellus conori* new species, paratype nymph: 17. Prosoma dorsal view; 18. Cucullus, dorsal view; 19. Opisthosoma, ventral view. Scales bars = 1.0 mm.

Material examined.—Brazil: *Amazonas*: Manaus, LBA Farm (Km 34, Br 174), 02°36′32″S, 60°12′32″W, 1 male, 12 August 2005, S.M. Ketelhut et al.; 1 female, 25 August 2006, F.B. Baccaro et al.; 1 nymph, 25 August 2006, F.B. Baccaro et al.; 1 nymph, 25 August 2006, F.B. Baccaro et al.; 2 nymphs, 16 May 2006, F.B. Baccaro et al.; 1 nymph, 15 November 2004, S.M. Ketelhut et al.; 3 nymphs, 8 August 2005, S.M. Ketelhut et al. Cabo Frio Farm, 02°25′S, 60°W, 1 nymph, 24 November 2005, S.M. Ketelhut et al.; 1 nymph, 24 July 2006, F.B. Baccaro et al. ZF 2 Farm (Km 14, Br 174), 02°35′20″S, 60°06′54″W, 3 nymphs, 20 October 2004, S.M. Ketelhut et al.; 1 nymph, 20 October 2004, S.M. Ketelhut et al. ZF 3 Farm (Km 37, Br 174), 02°35′55″S, 60°03′09″W, 1 nymph, 16 August 2005, S.M. Ketelhut et al.; 1 nymph, 16 August 2005, S.M. Ketelhut et al.; 1 nymph, 22 November 2005, S.M. Ketelhut et al.; 1 nymph, 20 July 2004, S.M. Ketelhut et al.; 1 nymph, 16 August 2005, S.M. Ketelhut et al.

Distribution.—This species is now known from Reserva Ducke (type locality), Tarumã-Mirim river (Adis et al. 1989), LBA Farm (Km 34, Br 174), ZF 2 Farm, ZF 3 Farm (Km 37, Br 174) and Cabo Frio Farm, located in Manaus municipality, Amazonas State, Brazil.

Relationships.—The *foedus* group was suggested by Platnick & Shadab (1977) as a monophyletic unit supported by the following synapomorphies: male cucullus with strong depression below its dorsal margin; expanded male basitarsus III; male with apophyses on trochanters of legs III and IV; and female spermathecae short and wide. For this study it is proposed that species included in this group also share a very inflated basitarsus (as long as wide) of leg III; a protuberance on the accessory piece of male leg III; and a large fixed male accessory piece forming an acute angle. *Cryptocellus foedus* was said by Platnick & Shadab (1977) to be closely related to the species *C. peckorum*, suggested as the plesiomorphic sister-taxon of *C. foedus*. However, they stated that *C. peckorum* and *C. lampeli* where not closely related to each other. *Cryptocellus peckorum* is herein included in a third assemblage of species, the *peckorum* group, which is composed of *C. peckorum*, *C. tarsilae*, *C. lampeli* and the new species *C. conori*. The basic

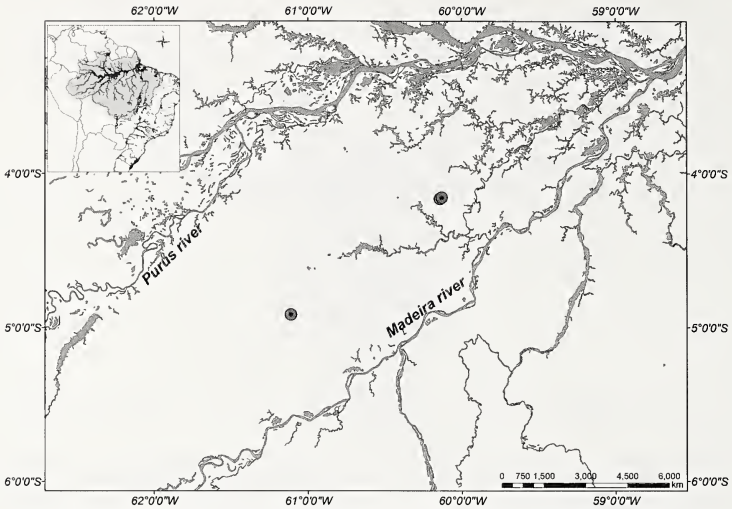


Figure 20.—Type locality of *Cryptocellus conori* new species, Careiro, Amazonas State, Brazil.

synapomorphies supporting this group are fixed male accessory piece of leg III thin; both movable and fixed piece curved, and with a sinuous contour; basitarsus of leg III moderately inflated (longer than wide).

The *Cryptocellus magnus* group was first suggested by Platnick & Paz (1979) based on species that share a massive and straight accessory piece of the male tarsal process. This character was hypothesized to be a derived character also present in *C. pseudocellatus*, known only from female specimens. *Cryptocellus glenoides* was originally included in the *magnus* group, as the most plesiomorphic lineage (Platnick & Paz 1979), but was later transferred to the *centralis* group which was based on a single apomorphic character, the presence of a peculiar anteroventral ledge on the tarsal process of male leg III, which is the basic synapomorphy for the *centralis* group, composed of 10 species (Platnick & Shadab 1981). We suggest that *C. platnicki* Botero-Trujillo & Pérez 2008 also belongs in the *centralis* group, based on its close relationship with *C. glenoides*. However, evidence for further synapomorphies is needed in order to state precisely the position of *C. glenoides* + *C. platnicki* in the *magnus* or *centralis* group (Platnick & Shadab 1981).

Among the five remaining species of *Cryptocellus*, three of them are here hypothesized to form a fifth group, the *adisi* group: *C. adisi*, *C. lisbethae*, and *C. florezi*. This group is based on a single shared character: the fixed accessory piece of male leg III is thin, curved and with a rounded contour. Platnick & García (2008) suggested the last species is more closely related to *C. lisbethae*, and that *C. adisi* resembles and could be related to *C. albosquamatus* (Platnick 1988). *Cryptocellus albosquamatus* is known only from female specimens, and its relationships and placement inside the established groups can only be properly done when and if the male of this species is found.

The current arrangement suggested in this paper for species included in the genus *Cryptocellus* is:

***Adisi* group**

Cryptocellus adisi Platnick 1988 (Brazil, Amazonas, Tarumã-Mirim river), known only from male.

Cryptocellus florezi Platnick & García 2008 (Colombia, Department of Caquetá), known from male and female.

Cryptocellus lisbethae González-Sponga 1998 (Venezuela, Bolívar), known from male and female.

***Centralis* group** (Platnick & Shadab 1981)

Cryptocellus centralis Fage 1921 (Costa Rica, Heredia, La Caja), known from male and female.

Cryptocellus chiriqui Platnick & Shadab 1981 (Panama, Chiriquí), known only from male.

Cryptocellus fagei Cooke & Shadab 1973 (Costa Rica, Golfito), known only from male.

Cryptocellus gamboa Platnick & Shadab 1981 (Panama, Canal Zone, Gamboa Pipeline), known from male and female.

Cryptocellus glenoides Cooke & Shadab 1973 (Colombia, Valle, 5 km of Delfina and Panama, Panama Province, Cerro Campana), known from male and female.

Cryptocellus goodnighti Platnick & Shadab 1981 (Costa Rica, Heredia, near Puerto Viejo de Sarapiqui), known only from male.

Cryptocellus hanseni Cooke & Shadab 1973 (Nicaragua and Honduras), known from male and female.

Cryptocellus isthmius Cooke & Shadab 1973 (Panama, Canal Zone, Gatun), known from male and female.

Cryptocellus luisedieri Botero-Trujillo & Pérez, 2009 (Colombia, Ipiales Municipality, Nariño Department), known only from male.

Cryptocellus osa Platnick & Shadab 1981 (Costa Rica, Puntarenas, Peninsula of Osa), known from male and female.

Cryptocellus platnicki Botero-Trujillo & Pérez 2008 (Colombia, Department of Chocó) – **dubious position** (Botero-Trujillo & Pérez 2008), known from male and female.

Cryptocellus striatipes Cooke & Shadab 1973 (Costa Rica, Limón, Colombiana), known from male and female.

***Foedus* group** (Platnick & Shadab 1977)

Cryptocellus abaporu Bonaldo & Pinto-da-Rocha 2003 (Brazil, Rondônia, Ji-Paraná), known from male and female.

Cryptocellus becki Platnick & Shadab 1977 (Brazil, Amazonas, near Manaus, Reserva Ducke), known from male and female.

Cryptocellus foedus Westwood 1874 (Brazil, Amazon, somewhere between Belém in Pará and São Paulo de Olivença, in Amazonas), known only from female.

Cryptocellus icamiabas Tourinho & Azevedo 2007 (Brazil, Amazonas, Presidente Figueiredo, Balbina), known only from male.

Cryptocellus simonis Hansen & Sørensen 1904 (Brazil, Pará, Belém), known from male and female.

Cryptocellus whitticki Platnick & Shadab 1977 (Guyana, Rupununi, New River district), known only from male.

***Magnus* group** (Platnick & Paz 1979)

Cryptocellus bordoni Dumitrescu & Juvara-Bals 1977 (Venezuela, Zulia), know from male and female.

Cryptocellus brignolii Cokendolpher 2000 (Suriname, Paramaribo), know only from male.

Cryptocellus magnus Ewing 1929 (Colombia, Magdalena), know only from female.

Cryptocellus narino Platnick & Paz 1979 (Colombia, Antioquia), known from male and female.

Cryptocellus pseudocellatus Roewer 1952 (Peru, Cajamarca), known only from female.

***Peckorum* group**

Cryptocellus conori new species (Brazil, Amazonas, Careiro), known from male and female.

Cryptocellus lampeli Cooke 1967 (British Guiana, Amatuk), known from male and female.

Cryptocellus peckorum Platnick & Shadab 1977 (Colombia, Amazonas, Leticia), known from male and female.

Cryptocellus tarsilae Pinto-da-Rocha & Bonldo 2007 (Brazil, Pará, National Forest (FLONA) of Carajás), known from male and female.

Nomina dubia

Cryptocellus leleupi Cooreman 1977 (Platnick & Paz 1979) (Ecuador, Oriente, Rio Negro), know only from nymph.

Cryptocellus emarginatus Ewing 1929 (Platnick & Shadab 1981) (Costa Rica, Cartago, Navarro farms), know only from nymph.

Remaining species

Cryptocellus albosquamatus Cooke 1967 (British Guiana, Amatuk), known only from female.

Cryptocellus bocas Platnick & Shadab 1981 (Panama, Quebrada Alicia), known only from female.

Cryptocellus verde Platnick & Shadab 1981 (Costa Rica, Puntarenas, Monteverde), known only from female.

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Patterns of abundance, habitat use and body size structure of *Phoneutria reidyi* and *P. fera* (Araneae: Ctenidae) in a Central Amazonian rainforest

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Abstract. *Phoneutria* is one of the most medically important spider genera; however, its ecology is poorly known. In Amazonian upland rainforests, there are two sympatric species of the genus *Phoneutria*, *P. reidyi* (F.O. Pickard-Cambridge 1897) and *P. fera* Perty 1833. For 15 months we collected data on the spatial distribution, use of habitat (activity on the ground or vegetation) and temporal changes in body size structure in a forest reserve near Manaus city in three distinct habitats: dense forest, located on the plateaus on yellow latossol; swamp forest, located in the valleys; and heath forest or "campinarana," on dry white sand soil in the Reserva Florestal Ducke. A total of 239 *P. reidyi* and 239 *P. fera* were captured in nocturnal searches during their period of activity. There were significant differences between the two species: 1) *P. reidyi* existed in higher abundance in the swamp forest than in the dense forest areas and was almost absent in the heath forest, while *P. fera* existed in similar abundance in the three habitats. 2) During their development, members of both species used the vegetation as an area of activity, but the subadults and adults of *P. reidyi* were less often found on the ground than the subadults and adults of *P. fera*. 3) *P. reidyi* more frequently used small or acaulescent palms as a substrate, and its abundance was directly related to the abundance of these palms, independent of the habitat, while *P. fera* did not show such relationship. 4) There was a strong temporal variation in the body size structure of the *P. reidyi* population indicating seasonal reproduction, but there was no evidence of seasonal reproduction by *P. fera*. We suggest that the differences in the use of habitat and in the seasonality of reproduction are related to the avoidance of intraguild predation between these species.

Keywords: Amazon, "banana-spider," coexistence, life cycle, microhabitat preferences, wandering spiders

Spiders of the genus *Phoneutria* are large nocturnal hunting species common in South American forests and in synanthropic areas close to these forests (Lucas 1988; Folly-Ramos et al. 1998). They are considered aggressive and among the medically most important spiders in the world, on the basis of the number of serious human accidents (Maretic 1987; Lucas 1988, 2002; Vetter & Isbister 2008). Despite their medical importance, little is known about their ecology, although they are frequently abundant in forests where they occur.

Bücherl (1969, 1980), Bücherl et al. (1969), Lucas (1969, 1988), Folly-Ramos et al. (1998), and Almeida et al. (2000) presented data on development, activity, seasonality of reproduction, and habitat use of *Phoneutria nigriventer* (Keyserling 1891). In southeastern Brazil, Bücherl (1969) and Lucas (1988) found that *Phoneutria keyserlingi* (F.O. Pickard-Cambridge 1897) and *P. nigriventer* reach maturity in three years, with a marked seasonal reproduction. These studies were based mainly on synanthropic populations and on animals kept in captivity. Until recently, nothing has been published on the ecology of the Amazonian species *Phoneutria fera* Perty 1833 and *Phoneutria reidyi* (F.O. Pickard-Cambridge 1897), although they have a large distribution in most "terra-firme" forests (Simó & Brescovit 2001). The present paper is part of the first intensive ecological research on the genus in undisturbed areas. In previous publications, we presented results on temporal variation in adult size and sexual dimorphism and notes on natural history (Gasnier et al. 2002; Gasnier et al. 2009).

Phoneutria reidyi and *P. fera* are among the most abundant large spider species in Amazonia. Healthy adults possibly have few enemies, but the juveniles are probably under constant risk. Most potential predators, such as army ants, spiders of the genus *Ctenus* and frogs, are more abundant on the ground (Vieira & Höfer 1994; Gasnier & Höfer 2001; Menin et al. 2008); therefore, the vegetation may be an important substrate, particularly for juveniles, to avoid predation. Both *Phoneutria* species are frequently found on plants with large leaves, especially acaulescent palms that may attract the spiders because their leaves can sustain their weight and transmit vibrations efficiently (Barth et al. 1988), or because of a higher availability of prey associated with the litter at its base (Vasconcelos 1990).

Differences in the use of habitat, phenology, and general behavior (including prey capture and reproductive behavior) are factors that contribute to the coexistence of spiders (Enders 1976; Uetz 1977; Turner & Polish 1979; Uetz 1991; Cutler & Jennings 1992; Polis & Holt 1992; Wise 1993; Morse 1997; Wise & Chen 1999; Denno et al. 2004; Rypstra & Samu 2005). Areas with the sympatric occurrence of two or more species are not common in the genus (Martins & Bertani 2007); only *P. reidyi* and *P. fera* have a large area of coexistence, apparently most of the Amazonian Region (Simó & Brescovit 2001). Our purpose was to study certain aspects of the ecology of *P. reidyi* and *P. fera* in a forest area, including factors that affect their abundance, use of habitat and life history, and to furnish the basis for understanding their coexistence.

METHODS

Study site and species.—The study was conducted in the Reserva Florestal Ducke, a 10,000 ha primary rainforest

reserve of the Instituto Nacional de Pesquisas da Amazônia (INPA). The fauna and flora of this reserve is one of the most heavily studied in Amazonia (Ribeiro et al. 1999; Adis 2002), including the spider fauna (Höfer & Brescovit 2001). We worked in the northern part of the reserve in the basins of the Barro Branco and Acará streams (2°55′00″–2°56′45″S, 59°57′08″–59°58′41″W). Well-drained clay soils in plateaus and slopes predominate in the basin of Barro Branco stream, with a dense forest (descriptions of vegetation in Guillaumet 1987), and well drained white sandy soils predominate in the basin of Acará stream, with a heath forest or "campinarana" offering a more open canopy than the dense forest. In both areas the soil is sandy and hydromorphic close to the streams, with vegetation called swamp forest or "baixio." In all areas the understory vegetation is relatively open. A description of the study area is presented in Gasnier & Höfer (2001). The average annual temperature is 25.6° C, and the average annual rainfall is 2480 mm. The rainy season occurs between December and May, with the rainiest months in March and April and the driest months from July to September (Marques-Filho et al. 1981). We made our observations and collections between June 1998 and August 1999.

We captured the spiders and observed them at night, with the help of headlamps strong enough to allow for observing spiders' eye reflection (including small individuals) up to a distance of approximately 15–20 m. The body of the spider is visible up to about 3–8 m, depending of the spider's size. The spiders could be located at a considerable height (up to 5 m), but were only captured at heights lower than 3 m. To avoid the effect of rain on the abundance estimates, we did not include data from nights with rain and nights after days with rain. We captured the spiders with glass or plastic vials proportional in size to the spiders (22–80 mm in diameter, 60–140 mm in height, and 20–60 mm opening) and preserved the specimens in 70% ethanol. The material is deposited in the Entomological Collection of INPA.

We initially identified the species in the laboratory based on the reproductive structures of adults (palps and epigyne). However, we realized that the ventral and dorsal color patterns of the body and stripes of the palps allowed us to discriminate among species in the field, including very small juveniles. The patterns are described and illustrated in Martins & Bertani (2007).

Censuses.—We used two types of census: one extensive census to evaluate variation in abundance of spiders in a large area including different habitats, and the other to compare abundance between dense forest on plateaus and swamp forest in valley areas. The extensive census consisted of 60 plots of about 50 × 10 m, separated by a distance of 100 m between plots in a trail of about 9 km inside an area of about 2 × 5 km. We collected spiders four times in each plot in June and October 1998, and in April and August 1999. One person searched for spiders from 0 to 3 m height for approximately 30 minutes in each plot. To investigate the influence of environmental factors on the abundance of the spiders, we counted the number of small or acaulescent palms (> 1 m diameter), collected samples of soil in each plot and calculated the volume of leaf litter. We measured the volume of leaf litter on the ground in the middle of the plot, placing the leaves from a 1-m^2 area in a graduated container. The volume from each plot was the mean of the measures made on two occasions.

Since the plots of the extensive census included few places with hydromorphic soils, we performed additional censuses comparing the dense forest areas on plateaus with the swamp forest areas on hydromorphic soils close to streams. We called these surveys plateau-swamp censuses. In these censuses, we searched for spiders in 15 plots on the plateau and in 15 plots in the swamp forest. The effort was standardized as a 2-h search in each plot by one person. The plateau-swamp censuses were made on four occasions, in August and November 1998 and in January and April 1999, but we collected spiders only once in each plot.

Spiders collected apart from the censuses (on other occasions or by someone following behind the person searching) were not considered in the comparisons of abundance among habitats, but were included in the analysis of vertical distribution and population structure. For each spider collected, we recorded the species, size (prosoma length), sex (if adult), and the type and height of the substrate. On the first excursion, small juveniles were not collected because we could not identify small *Phoneutria*.

Statistical Analyses.—The analysis of abundance in a sequence of plots helps to evaluate variation at different scales when the sample unit is not discrete and natural (Ludwig & Reynolds 1988), and to propose hypotheses on factors that affect the abundance. The number of spiders in each plot was low (up to 5); therefore, we used non-parametric tests (Mann-Whitney *U*-test and Spearman rank correlation, r_s). The linear regression between the number of spiders and the number of palms was modeled with Reduced Major Axis because the values of the independent variable were random (Sokal & Rohlf 1995). The interspecific correlation of *P. reidyi* and *P. fera* was tested with Spearman rank correlation, and the interspecific association was tested with Yates corrected χ^2 test in a 2 × 2 contingency table with the presence/absence of both species (Ludwig & Reynolds 1988). We used the equality of proportions test to verify whether proportions of spiders on the ground or vegetation differed between species. The seasonality of reproduction was evaluated with a Kolmogorov-Smirnov test, comparing the distribution of body sizes graphically and testing the difference in sizes of juveniles in October 1998 and April 1999, because these were months with large data sets and were six months apart. The statistical package used was SYSTAT 12© (Wilkinson 1990).

RESULTS

Abundance Patterns.—A total of 239 *P. reidyi*, (181 juveniles, 36 adult males, and 22 adult females) and 239 *P. fera* (respectively 181, 27 and 31) was recorded. However, the proportions of species were different between the two types of censuses. In the 60 plots on the trail of the extensive census, made in areas where well-drained soils predominated, 56 spiders were *P. reidyi* and 108 were *P. fera*. In the plateau-swamp census, made in 15 areas of well-drained soil and 15 areas of swamp forest, 136 spiders were *P. reidyi* and 55 were *P. fera*. The spiders collected outside the censuses were 47 *P. reidyi* and 76 *P. fera*.

In the extensive census, the patterns of abundance were similar within each species, and different between species in

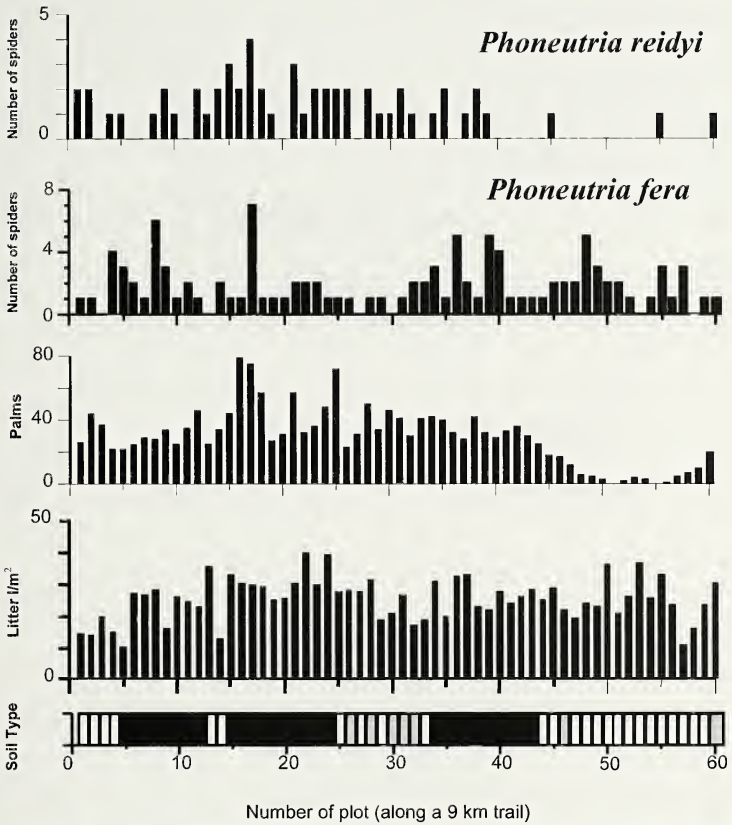

Figure 1.—Superposition of graphs of abundance, showing both species and characteristics of the habitat (number of palms, volume of leaf litter, and type of soil) along the line of extensive census. Each bar corresponds to a transect of 50 m. The soils were categorized as sandy (white), hydromorphic (gray) and clayey (black), and they are closely related to the vegetation types (see Methods).

the four counts throughout one year. *P. reidyi*'s pattern was marked by a high abundance (1.36 spiders/100 m) in positions 1–39 and low abundance (0.14/100 m) in the basin of Acará stream (positions 40–60 in Fig. 1), in an area where heath forest over sandy soils predominated. This zone had lower abundances of small or acaulescent palms, but similar amounts of leaf litter compared to the other areas. Compared to *P. reidyi*, *P. fera* had a relatively homogeneous abundance along the sequence of plots (1.8/100 m).

In addition, we compared the abundances of spiders between the habitats "dense forest" and "swamp forest", using the plateau-swamp census samples. *P. reidyi* was more abundant in the swamp forest (Mann-Whitney *U*-test, $U = 117$, $P = 0.036$), where palms predominate. The abundance of *P. fera* did not differ significantly between these two habitats (Mann-Whitney *U*-test, $U = 67$, $P = 0.051$), with a tendency for smaller numbers in the swamp forest. This difference suggested that the abundance of small or acaulescent palms was an important factor.

To test the correlation between abundance of palms and abundance of spiders, we used data from the extensive census samples. There was a positive correlation between the number of *P. reidyi* and the number of palms (Spearman rank correlation, $r_s = 0.63$, $n = 60$, $P < 0.001$; Fig. 2). As shown above, this relationship is in part a result of differences between habitats for the abundance of palms and the abundance of *P. reidyi*, which is weak evidence of a causal relationship. Therefore, we performed two additional tests for the relationship between the number of *P. reidyi* and the number of palms, separated by habitat, only in areas with dense forest (Spearman rank correlation, $r_s = 0.67$, $n = 28$, $P < 0.001$) and only in areas with heath forest vegetation (Spearman rank correlation, $r_s = 0.50$, $n = 25$, $P = 0.003$) (sample size in swamp forest was low for this test). These tests show that this positive correlation is

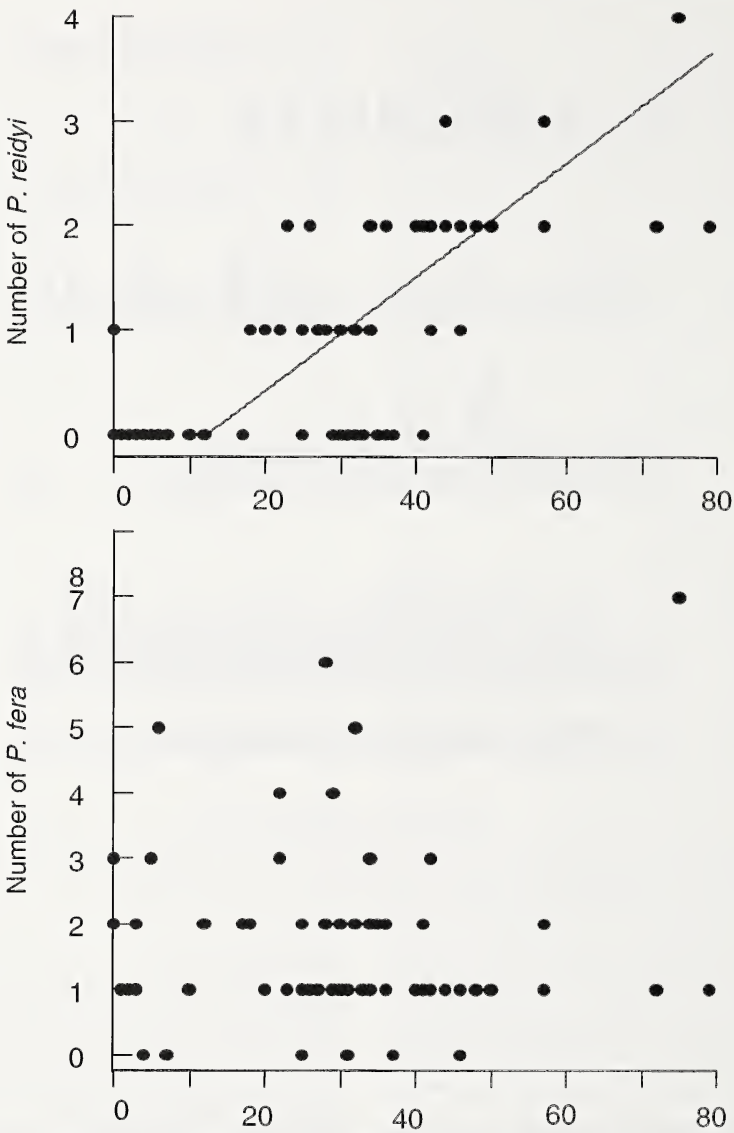

Figure 2.—Relationship between the abundance of palms and the number of spiders in each sample unit. The relationship was significant only for *P. reidyi*, for which a regression line is shown (Reduced Major Axis Regression, $Y = -0.671 + 0.0545X$).

independent of the type of habitat for *P. reidyi*. The number of *P. fera* and the number of palms did not differ significantly in the extensive census plots (Spearman rank correlation, $r_s = -0.14$, $n = 60$, $P = 0.28$).

We tested the correlation between leaf litter volume and the number of spiders using the extensive census data because the abundance of prey and availability of refuges for spiders may be affected by the volume of leaf litter. We found no

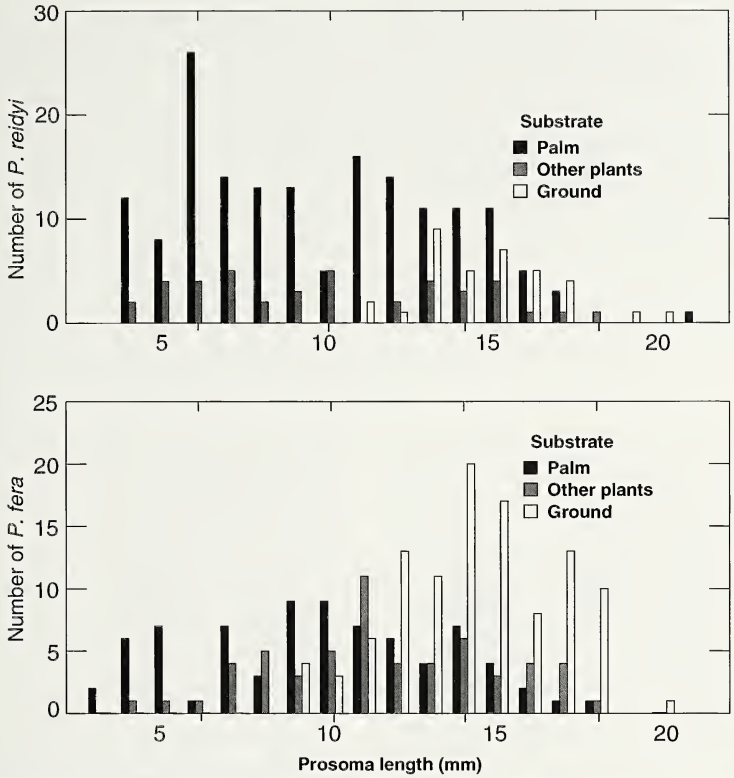

Figure 3.—Frequency of size (prosoma length) categories for *P. reidyi* and *P. fera* found on three types of substrate.

significant relationship between the number of spiders and the amount of leaf litter for *P. reidyi* (Spearman rank correlation, $r_s = 0.15$, $n = 60$, $P = 0.23$) or *P. fera* (Spearman rank correlation, $r_s = -0.05$, $n = 60$, $P = 0.72$).

To evaluate the interspecific association between these species, we used the sample units of the extensive census ($n = 60$) and of the plateau-swamp census ($n = 30$). There was no significant correlation between the abundance of *P. reidyi* and *P. fera* (Spearman rank correlation, $r_s = -0.04$, $n = 90$, $P = 0.72$), nor in the presence/absence (P/A) of the species (PP = 51, PA = 24, AP = 11, AA = 4; $\chi^2 = 0.01$, $P = 0.91$).

Use of the habitat.—Use of habitat changed substantially during the development of both spider species. Juveniles with prosoma length < 9 mm were only found on the vegetation, and spiders gradually increased their use of the ground until they reached adult size (Fig. 3). However, there were differences between species. Use of the vegetation was still preponderant for *P. reidyi* with PL > 12mm, while most *P. fera* of this size were found on the ground. Furthermore, *P. reidyi* of all spider sizes used small or acaulescent palms much more frequently than other plants, while medium and large *P. fera* were found on both palms and other plants in similar frequency. A higher proportion of *P. fera* with PL >12 mm was found on the ground (Proportions test, 45% of 88 *P. reidyi* and 67% of 121 *P. fera*; $Z = 3.10$, $P = 0.002$). This difference was independent of the habitat because it was still significant when we restricted the data to swamp forest (Proportions test, 35% of 23 *P. reidyi* and 75% of 12 *P. fera*; $Z = 2.25$, $P = 0.02$) or dense forest (Proportions test, 49% of 61 *P. reidyi* and 68% of 88 *P. fera*; $Z = 2.33$, $P = 0.02$) (only 4 *P. reidyi* were found in the heath forest, which was not sufficient for a comparison).

The height at which spiders were found on the vegetation (i.e., height > 0 cm) did not differ significantly between adult males (median = 120 cm, $Q_{25} = 40$, $Q_{75} = 150$) and females (median = 45 cm, $Q_{25} = 37$, $Q_{75} = 57$) of *P. reidyi* (Mann-Whitney *U*-test, $U = 109$, $P = 0.08$) or between adult males (median = 30 cm, $Q_{25} = 19.5$, $Q_{75} = 49.5$) and females (median = 40 cm, $Q_{25} = 12$, $Q_{75} = 113$) of *P. fera* (Mann-Whitney *U*-test, $U = 40$, $P = 0.74$). There was no difference in the height of juveniles between *P. reidyi* (median = 85 cm, $Q_{25} = 49$, $Q_{75} = 150$) and *P. fera* (median = 71 cm, $Q_{25} = 40$, $Q_{75} = 134$) (Mann-Whitney *U*-test, $U = 10{,}024$, $P = 0.13$); nor

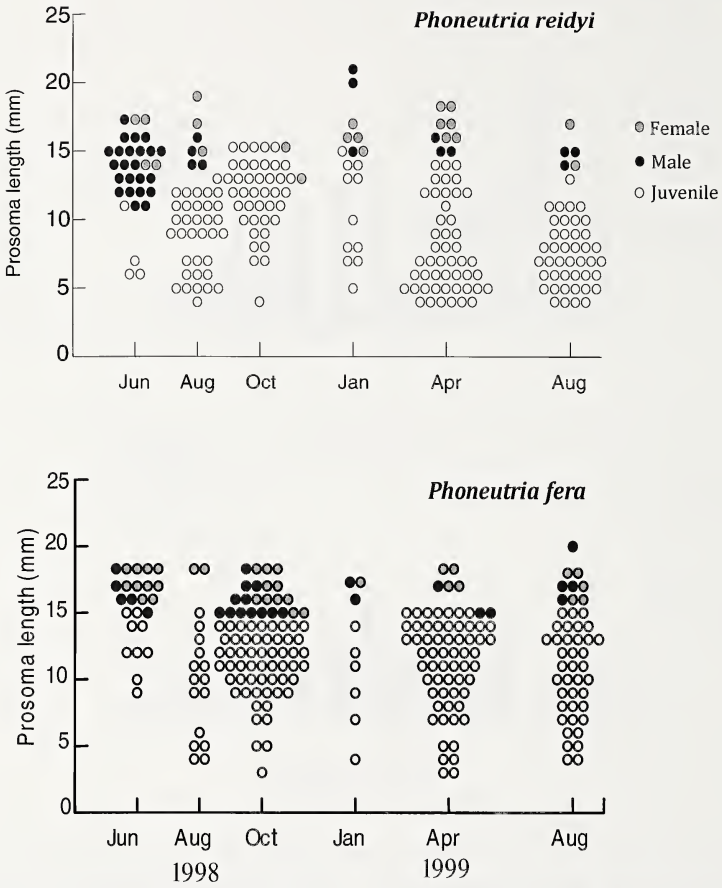

Figure 4.—Distribution of sizes of *P. reidyi* and *P. fera* on each of six collection dates during two years.

between females of the two species (Mann-Whitney *U*-test, $U = 42$, $P = 0.56$). However, male *P. reidyi* were found in higher places than male *P. fera* (Mann-Whitney *U* test, $U = 169$, $P < 0.001$).

Structure of body size.—There was strong temporal variation in the structure of body size of *P. reidyi* (Fig. 4). Comparing data from October 1998 and April 1999, we found a significant difference (Kolmogorov-Smirnov test, $D = 0.57$, $P < 0.001$). This variation indicates a marked seasonal reproduction for *P. reidyi*. Another indication of seasonal reproduction was the high proportion of males captured in June 1998 (23♂♂: 4♀♀), most of them (93%) being on the ground, which, in this species, could indicate that they were searching for females.

In *P. fera*, the structure of sizes remained relatively constant during the study (Fig. 4). Comparing data from October 1998 and April 1999, we found no significant difference (Kolmogorov-Smirnov test, $D = 0.15$, $P = 0.58$). Apparently, these spiders reproduce throughout the year. Another indication of continuous reproduction in *P. fera* was that the sex ratio did not change much throughout the year, and both males and females were found on the ground in similar proportions (56% and 45% respectively).

DISCUSSION

The abundance of small and acaulescent palms correlated with the abundance of *P. reidyi* within habitats; consequently, this factor may explain why this species is abundant in swamp forests, where the palms are abundant and why they are rare in the heath forest, where the palms are almost absent. The association between *Phoneutria* and plants with large leaves, as we have found for *P. reidyi*, has been documented in previous

papers (Schiapelli & Gerschman 1972; Bücherl 1980; Lucas 1988). Therefore, more remarkable was the absence of a relationship between the abundance of *P. fera*, collected in similar numbers in the same area, with the abundance of palms.

We propose that the preponderance in use of the vegetation by juveniles of both species is an adaptation to avoid their common ground predators, and that the adults and subadults of *P. reidyi* use the vegetation more frequently, mainly to avoid predation by adults and subadults of *P. fera* on the ground. Barth et al. (1988), working with spiders of the genus *Cupiennius*, found that the palms are probably a safe place to stay because a spider is less visible and more able to sense vibrations of an approaching predator. Small juvenile *P. fera* were almost always on the vegetation; only individuals with a prosoma length greater than 8 mm were found on the ground. This is about the mean size of adults of two important potential predators, *Ctenus amphora* Mello-Leitao 1930 and *Ctenus crulsi* Mello-Leitao 1930, the most abundant medium-sized wandering spiders on the ground (Gasnier et al. 2002). Once *P. fera* spiders grow larger, their dispersal on the ground may be an advantage, because the *Ctenus* spiders will be smaller than them and thus become potential prey. We made no observations of *Ctenus* preying on *Phoneutria*, probably because small individuals were rare on the ground, but similar wandering spiders are among the main prey of *Ctenus*, and we observed that *Ctenus* was among the main prey of medium-sized to large *Phoneutria*. A similar pattern was noted with *P. reidyi*, but they also have *P. fera* as a larger predator on the ground. The mean prosoma length of adult *P. reidyi* (14.4 mm in males and 15.9 mm in females: Gasnier et al. 2002) is inferior to the mean prosoma length of *P. fera* (16.2 mm in males and 16.8 mm in females). Smaller spiders are probably more vulnerable to intraguild predation (Polis et al. 1989) and, consequently, less exposed (Johnson & Sih 2007), which would explain the more intensive use of the vegetation by *P. reidyi*.

Direct evidence from a field experiment is necessary to demonstrate cases of coevolutionary divergence (Connell 1980) like the differentiation in use of the habitat suggested above. Meanwhile, there are additional arguments and evidence to sustain the hypothesis that the interaction between these two species, and possibly among other species of *Phoneutria*, is a relevant factor in their ecology. 1) The absence of a negative association between these sympatric species is not incompatible with this hypothesis because it is possible that coexistence in the present may have been facilitated by differentiation in the use of vegetation under intraguild predation pressure in the past. 2) The seasonality in reproduction of *P. reidyi* is consistent with this hypothesis because males searching for females probably have to disperse more frequently on the ground, and limiting this behavior to a part of the year could be an adaptation to prevent predation by *P. fera*. 3) *P. boliviensis* (F.O. Pickard-Cambridge 1897) is another Amazonian species with the smallest adults of the genus in central Amazonia. We have never seen it in "terra firme" forests, but it is relatively common in periodically inundated forests (T. Gasnier, pers. obs.). 4) Martins & Bertani (2007) showed that sympatry is practically restricted to the distribution limits of four species of *Phoneutria* in southeastern Brazil (only *P. pertyi* [F.O. Pickard-Cambridge 1897] was sympatric with other species). These contiguous allopatry patterns do not prove, but are consistent with, the importance of intraguild predation in the genus. Field experiments and study of the use of the habitat by sympatric and allopatric populations of *Phoneutria* species are necessary to verify these hypotheses and understand the ecology and evolution of this genus.

Phoneutria may be considered key species in the forests where they occur. Most studies on *Phoneutria* were based on few individuals, probably because adults are not easy to find (Almeida et al. 2000). However, much data on abundance, distribution, and behavior may be acquired when juveniles are included in the study (e.g., Folly-Ramos et al. 1998; present study). Therefore, together with other ctenids, these spiders may be good indicators of disturbance in forest fragments (Jocqué et al. 2005). The ecology of *Phoneutria* is not only important because of its medical importance. Comparative studies may also help to understand the importance of these predators in Neotropical forests.

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Ultraviolet light detection: a function of scorpion fluorescence

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Abstract. The hypothesis that fluorescence in scorpions functions in the detection of ultraviolet light was tested. We reduced the fluorescence of scorpions by prolonged exposure to ultraviolet light on a 16:8 h light:dark cycle and compared their activity levels and light environment choices to unmodified scorpions in simple arenas that were half in shadow and half exposed to light. Three different lighting conditions were tested: infrared (IR) light only, IR + ultraviolet light and IR + white light. Treatments were illuminated by infrared light for videotaping. Activity level was measured by the number of transitions from the exposed to shadowed regions, and choice was measured by the percentage of time spent in the shadowed portion of the arena. Under IR + ultraviolet light, fluorescent scorpions reduced their activity levels and the variance in habitat choice increased, compared with reduced-fluorescence scorpions. There were no differences between fluorescent and non-fluorescent scorpions in the IR only condition or in the IR + white light condition. This is interpreted as evidence that fluorescence aids in the detection of and response to ultraviolet light, and possible implications of this result in natural habitats are discussed. This is the first experimental demonstration of a possible function for scorpion fluorescence.

Keywords: Moonlight avoidance, habitat choice, light responses

The fluorescence of scorpion cuticles is a well known, but little understood, phenomenon. Although two molecules associated with scorpion fluorescence have been isolated and identified – a ß-carboline (Stachel et al. 1999) and 4-methyl, 7-hydroxycoumarin (Frost et al. 2001) – no function of scorpion fluorescence has previously been demonstrated. This article reports the first empirical support for a function for scorpion fluorescence.

Several specific hypotheses regarding possible functions of scorpion fluorescence have been put forward, including the possibility that fluorescence functions in ultraviolet (UV) light detection (Blass & Gaffin 2008), mate identification and species discrimination (Kloock 2008), luring of prey (Kloock 2005), light amplification (Camp & Gaffin 1999), or as a sunscreen (Lourenço & Cloudsley-Thompson 1996). Some authors have hypothesized that fluorescence has no function, being either a relict trait (Frost et al. 2001) or correlated with some other functional aspect of the molecules responsible (i.e., sclerotization: Stachel et al. 1999). Those functions that have been tested to date have not received empirical support (Kloock 2005, 2008).

A recent methodological development, the ability to significantly reduce fluorescence from live scorpions (Kloock 2009), makes new tests of functional hypotheses possible by allowing us to compare the behavior of fluorescent and reduced-fluorescence scorpions in different situations. We report here on a series of experiments supporting the hypothesis that scorpion fluorescence functions in the detection of ultraviolet light.

METHODS

Specimens.—Female *Paruroctonus becki* (Gertsch & Allred 1965) (Vaejovidae) were collected July–September 2008 in Kern County, California (voucher specimens deposited at the California Academy of Sciences, San Francisco). They were maintained in the laboratory in small, foam-plugged plastic vials, fed mealworm larvae and misted with water once per week until beginning the fluorescence reduction procedure. Only female scorpions were used in the experiments.

Fluorescence reduction.—We used a modification of the method for reducing the fluorescence from living scorpions presented in Kloock (2009) to produce a group of scorpions with significantly reduced fluorescence. The original method involved exposing scorpions for 24 h/day to low level (11μW/cm^2) UV lights (two 40 W fluorescent GE black light tubes) until fluorescence faded (~ 4.5 wk). Because of the potential effect of constant light exposure on scorpion circadian rhythms (Fleissner 1977a, b, c; Schliwa & Fleissner 1980; Fleissner & Fleissner 2001), and therefore behavior, we modified this technique by exposing the scorpions on a 16:8 h light:dark cycle. This extended the time for complete loss of visible fluorescence to ~6 wk, but otherwise resulted in an effect similar to that reported by Kloock (2009).

During UV exposure, scorpions were housed in small, open-topped plastic containers (13 cm length × 10 cm width × 7 cm height) with 12 ml of native soil: enough to provide a substrate, but insufficient for scorpions to bury themselves for protection from UV exposure. Scorpions were fed a single mealworm larva twice a week: if they failed to eat the larva, it was removed and a fresh larva provided at each feeding. Scorpions were also provided water twice a week by lightly misting the soil surface. Scorpions were maintained on this schedule until all experiments using them were completed.

Control scorpions.—Control and reduced-fluorescence scorpions were kept in identical containers with the same amount of soil and on identical feeding, watering, and lighting schedules with the exception that a layer of UV blocking film (Edmund Optics NT39-426) was interposed between the UV light source and the scorpions. Control and experimental scorpions were kept in a common environmental chamber with the same UV lights during UV exposure, so that environmental conditions were identical for all scorpions. Control scorpions showed no visible reduction in fluorescence over the course of the experiments.

Basic setup.—The basic experimental design owes considerable debt to Blass and Gaffin (2008), whose methods we have adapted and simplified for our purposes. All three experiments share the basic feature of placing scorpions in 14-cm diam.

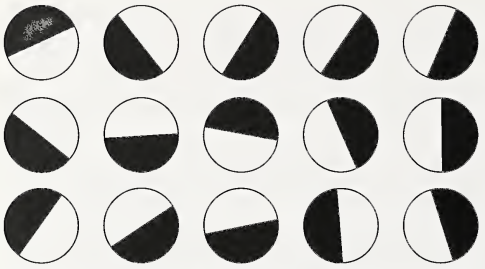

Figure 1.—Schematic of the 3 × 5 array of half-painted Petri dishes used in the experiment, showing a typical random orientation of dark and light halves.

Petri dishes, which had one-half of their exterior surface (top and bottom) painted over with water-based, non-toxic black paint (Fig. 1). No paint was on the interior surface of the Petri dish to act as a possible cue for the scorpions. Petri dishes were washed with 70% ethanol and allowed to dry for more than 20 h before each use to remove any potential chemical cues previous occupants may have deposited (Steinmetz et al. 2004).

We placed a single scorpion, either fluorescence-reduced or control, in each Petri dish, aligning the top and bottom halves so that half of the surface area of the Petri dish allowed light in, while the other half served as a light refuge. Petri dishes with scorpions were placed with the light and dark halves randomly oriented on a clear Plexiglas observation deck (Fig. 1) with an infrared sensitive video camera below and six infrared light emitting diodes (830 ± 35 nm) placed on the sides of the observation deck and reflecting off a light blue panel attached to the ceiling. This provided diffuse infrared illumination for videotaping. Scorpions have previously been shown not to respond to infrared illumination (Blass & Gaffin 2008).

Control and reduced-fluorescence scorpions were alternated in a 15 Petri dish array (three rows, five columns) and the camera adjusted to allow good visualization of all scorpions. A monitor in another room was used to ensure that all Petri dishes were easily observed, and all experiments were recorded on 42-min videotapes, which set the length of each trial. Two variables were recorded from the videotape analysis: percent time spent in the dark-covered half and the number of times scorpions moved from the exposed side to the covered side of the Petri dish (transitions). The percent time in the dark half acts as a measure of habitat choice, while the number of transitions acts as a simple measure of activity level.

In all experiments scorpions were allowed to acclimate to the array and lighting conditions for one hour before videotaping began, and the acclimation period began within 15 min of laboratory "sunset" to target the typical scorpion activity period (Hadley & Williams 1968). Just prior to the initiation of each experiment, each scorpion was moved into the clear portion of the Petri dish by gently tilting the dish toward the clear side; this ensured that all scorpions were visible at the beginning of the trial, and that they all experienced the lighting conditions, at least briefly, during the trial. Illumination other than the infrared needed for videotaping differed in the experiments that follow.

Experiments 1 and 2.—The same set of 15 control and 15 reduced-fluorescence scorpions was used for experiments 1 and 2. The order of presentation was randomized, with eight of the control and seven of the reduced-fluorescence scorpions receiving IR only illumination first (Experiment 1). Seven control and eight reduced-fluorescence scorpions received IR+UV illumination first (Experiment 2). The scorpions were then exposed to the alternate illumination, so that each experiment achieved a total sample size of 15 fluorescent and 15 reduced-fluorescence scorpions. All trials were completed over a four-night period.

Experiment 1: No illumination. This experiment constitutes a control for possible effects of the fluorescent reduction treatment. We placed scorpions in the standard experimental setup described above and videotaped them for 42 min. Fluorescence reduction should have no effect in this environment. If control and fluorescence-reduced scorpions exhibit significant differences in this experiment, then behaviors being measured were changed by the fluorescence reduction procedure itself.

Experiment 2: IR + UV illumination. As in Experiment 1, scorpions were placed in the standard experimental setup, but UV illumination was provided by a rectangular array (52 cm × 67 cm) of nine UV LEDs (Roithner-Lasertek RLT360-1.0-15, peak emission wavelength = 361 nm, spectral ½-width = 10 nm, viewing ½-angle = 15d) equally spaced. The array was placed 1.2 m above the observation deck, allowing room for the light from each LED to overlap, providing diffuse illumination across the observation deck. Although these LEDs caused scorpions to fluoresce at short distances, at a distance of 1.2 m, scorpions under the array did not visibly fluoresce; measurement of UV power using a Mannix UV-340 light meter (range = 290–390 nm) yielded < 1 $\mu W/cm^2$. Although fluorescence was not detectable by human vision, the question we are asking here is whether or not it is detectable by scorpions, whose vision is much more sensitive to low light levels than humans' (Fleissner 1977c). Ultraviolet intensity was kept very low to mimic natural nocturnal conditions. If fluorescence functions in UV light detection, we expect to see significant differences between control and fluorescence-reduced scorpions in this experiment.

Experiment 3.—IR + White light: The expected results of Experiment 2 under the hypothesis that fluorescence functions in UV light detection are also consistent with the possibility that the fluorescence-reduced scorpions suffered damage to the retina and/or the extra-ocular light sense (Zwicky 1970) during their exposure to UV light. To test this possibility we initiated a new experiment using white light. The basic experiment was identical to experiments 1 and 2, except that additional illumination was supplied by white light from two 40W fluorescent tubes. Rather than being placed directly over the scorpions, the lights were placed to the side to provide diffuse illumination because of the higher power of these lights. These lights did not produce measurable UV light on the observation deck. This experiment used novel scorpions, treated identically to those used in experiments 1 and 2, but with a slightly smaller sample size due to the death of some of the scorpions in this group during the preparation period. For

Table 1.—Summary of transitions between light and dark regions of the Petri dish by fluorescence in experiments 1–3. All data presented use the transformation (transitions$^{-1/2}$).

	Experiment 1 (IR only)		Experiment 2 (IR+UV Light)		Experiment 3 (IR+White light)	
Light condition	Control (fluorescent) (n = 15)	Fluorescence reduced (n = 15)	Control (fluorescent) (n = 15)	Fluorescence reduced (n = 15)	Control (fluorescent) (n = 14)	Fluorescence reduced (n = 13)
Transitions (mean ± SD)	4.1 ± 3.2	4.8 ± 2.2	3.0 ± 2.0	4.7 ± 2.2	1.2 ± 0.43	1.3 ± 0.44
95% CI:						
Lower limit	2.3	3.6	1.9	3.5	1.0	1.1
Upper limit	5.9	6.1	4.1	5.9	1.5	1.6
Levene's test for variances	F = 2.447, P = 0.129		F = 0.182, P = 0.673.		– Non-normally distributed	
Test for means	Equal variances t-test		Equal variances t-test		Mann-Whitney U-test	
Test statistic	t = 0.751, df = 28		t = 2.244, df = 28		U = 90.0	
P	0.459		0.033		0.961	

Experiment 3, there were 14 control scorpions and 13 reduced-fluorescence scorpions. If scorpion vision was damaged by the fluorescence reduction treatment, we should see significant differences between control and reduced-fluorescence scorpions, in a pattern similar that of Experiment 2.

Statistical analysis.—Evaluation of the hypothesis that fluorescence affects the response to UV does not depend on differences between the light treatments, but rather on the overall pattern of differences between control and reduced-fluorescence scorpions within each of the three experiments. Thus we are not interested in differences between light treatments, but instead in the differences between control and reduced-fluorescence scorpions within each experiment. The number of transitions and the percentage of time spent in the dark were analyzed separately in each experiment to determine if significant differences existed. Both variables within each experiment were analyzed for normality using the Kolmogorov-Smirnov test for normality, and homogeneity of variances was tested using Levene's test for equality of variances. Means within each experiment were compared with either the Mann-Whitney U test (for non-normally distributed data) or a t-test (for normally distributed data), with assumptions of equal or unequal variances as dictated by the data structure. Given that the number of transitions is expected to have a Poisson distribution, the square root transform was applied a priori to normalize this variable in all tests.

RESULTS

The number of transitions$^{1/2}$ in the IR + white light condition was not normally distributed (Kolmogorov-Smirnov Z = 1.993, P = 0.001). All other Kolmogorov-Smirnov tests of normality showed that the data were normally distributed (For % dark: IR only Z = 0.500, P = 0.964; IR+UV light, Z = 0.681, P = 0.743; IR + white light, Z = 1.088, P = 0.187. For transitions$^{-1/2}$: IR only, Z = 0.834, P = 0.490; IR +UV light, Z = 0.683, P = 0.740).

Table 1 presents the data and results of statistical tests on the number of transitions between the light and dark sides of the Petri dish. Levene's test for equality of variances revealed no differences between variances in experiments 1 and 2. Therefore, t-tests assuming equal variance were used to compare fluorescent and non-fluorescent scorpions while the non-parametric Mann-Whitney U test was used for Experiment 3 due to the non-normality of transitions$^{1/2}$ in white light. Fluorescent and reduced-fluorescence scorpions did not differ in the number of transitions when either IR only or white light was present, but did differ when UV light was present (Table 1). Fluorescent scorpions made fewer transitions when exposed to UV light than did fluorescence- reduced scorpions.

Table 2 presents the data and results of statistical tests on the percentage of time spent in the darkened half of the Petri dish (% dark). Levene's test for equality of variances showed no difference in the variance between fluorescent and reduced-fluorescence scorpions in either the IR only or white light experiments, but a significant difference in variance in the UV light experiment was found. Thus t-tests assuming equal variance were applied to experiments 1 and 3, while for Experiment 2, equal variances were not assumed. There were no significant differences between the means of fluorescent and reduced-fluorescence scorpions for % dark in any of the experiments. Confidence intervals all include 50%, as expected if scorpions exhibit no preference for either side of the Petri dish.

Because of the difference in variances detected in Experiment 2, we decided to look more closely at the distribution of the percentage of time spent in the dark to see, post hoc, if any patterns emerged. Inspection of histograms suggested that the larger variation in fluorescent scorpions was caused by the tendency of these scorpions to stay in either the light or dark half of the Petri dish, with few of these scorpions having intermediate values of % dark. A simple categorization of % dark into "extreme" (< 25% or > 75%) vs. "moderate" (between 25% and 75%) values reveals this. With only IR light (Experiment 1), scorpions showed no tendency toward extreme values, regardless of fluorescence condition. Both fluorescent and reduced-fluorescence scorpions showed 7 "extreme" and 8 "moderate" values, (χ^2 = 0.067, df = 1, P = 0.80). With UV light present (Experiment 2) reduced-fluorescence scorpions showed no tendency toward extremes (6 "extreme" and 9 "moderate", χ^2 = 0.60, df = 1, P = 0.44), while fluorescent scorpions displayed a strong tendency toward extreme values (13 extreme, 2 moderate, χ^2 = 8.1, df = 1, P = 0.0045). Scorpions exposed to white light, despite reduced activity levels (Table 1) also showed no preference for extremes (Reduced-fluorescence; 8 extreme, 5 moderate, χ^2 =

Table 2.—Summary of the percentage of time spent in the dark half of the Petri dish by fluorescence in experiments 1–3.

	Experiment 1 (IR only)		Experiment 2 (IR+UV light)		Experiment 3 (IR+White light)	
Light condition	Control (fluorescent) (n = 15)	Fluorescence reduced (n = 15)	Control (fluorescent) (n = 15)	Fluorescence reduced (n = 15)	Control (fluorescent) (n = 14)	Fluorescence reduced (n = 13)
Mean % Dark (mean ± SD)	44.8 ± 32.8	40.4 ± 25.3	55.5 ± 37.9	56.8 ± 25.3	43.9 ± 39.6	44.2 ± 38.1
95% CI:						
Lower limit	26.7	25.3	34.5	42.8	34.5	21.2
Upper limit	63.0	54.4	76.4	70.9	76.4	67.3
Levene's test for variances	F = 1.104, P = 0.302		F = 7.945, P = 0.009		F = 0.192, P = 0.655	
t-test assumption	Equal variances		Variances not equal		Equal variances	
t (df)	0.418 (28)		0.118 (28)		0.022 (25)	
P	0.679		0.907		0.983	

0.69, P = 0.41: Fluorescent; 9 extreme, 5 moderate, χ^2 = 1.1, P = 0.29). We should caution, however, that both the small sample size for χ^2 and post-hoc nature of this analysis call for conservative use of this information in interpretation.

DISCUSSION

These results support the hypothesis that scorpion fluorescence serves as a means for the detection of ultraviolet (UV) light at very low levels. Significant differences between the activity levels of fluorescent and reduced-fluorescence scorpions occurred only in the presence of UV light, with fluorescent scorpions changing their behavior by reducing their activity level (Table 1). Additionally, tests on variances in % dark revealed a difference between fluorescent and reduced-fluorescence scorpions only under UV light (Table 2).

Although a difference in the variance in the % dark under UV light was detected, there was no difference in the mean time spent in the two sides of the dish by fluorescent and reduced-fluorescence scorpions; in fact, no differences in the mean % dark were observed in any experiment (Table 2). No preference for either side of the Petri dish was observed in any of the conditions, as all confidence intervals include the random expectation of 50% (Table 2). Although fluorescent scorpions reduced their activity levels in response to UV light, this did not change the mean time they spent in the different light environments. In other words, the change in activity level did not result in a change in the average use of the environment. The obvious question then is whether this response to UV light has any value in a natural environment.

Scorpion surface activity is generally higher during moonless nights than moonlit nights (Skutelsky 1996), and nocturnal UV light levels correlate to moon phase (Silberglied 1979). Thus, it is possible that UV light acts as a cue for moonlight avoidance. Blass & Gaffin (2008) demonstrated avoidance of UV light, but the data here indicate no avoidance of UV (Table 1). It is very likely that the low level of UV light used in this experiment did not reach a threshold for avoidance behavior. Blass & Gaffin (2008) used a greater intensity of UV light in their experiment (0.9 lux), so were more likely to observe avoidance. More work needs to be done to determine more precisely the intensity required to elicit avoidance behavior, and whether this differs between fluorescent and reduced-fluorescence scorpions. In order to determine if avoiding UV light results in moonlight avoidance, experiments comparing fluorescent and reduced-fluorescence scorpions in moonlight and UV-filtered moonlight are necessary. Conducting tests under natural illumination conditions is a natural follow-up to the current experiment that would help determine whether simple moonlight avoidance is the main function of fluorescence. Another interesting experiment could involve measuring individual scorpion responses to UV light before reducing their fluorescence, then reducing their fluorescence and re-measuring, and finally, measuring a third time after fluorescence recovers. This would establish that the behavior of individuals changes in response to the manipulation. Unfortunately, the time involved in this set of manipulations (~ 6 weeks to remove fluorescence, plus several weeks to recover full fluorescence) would introduce the potential confounding of seasonal differences in responses.

The decision of whether to forage in moonlight or seek cover is influenced by factors other than UV light levels. Therefore, we must consider the possibility that the lack of UV light avoidance displayed in this experiment resulted from differences in decisions by individual scorpions about whether or not to seek cover. For example, Skutelsky (1996) found that scorpions with lower body mass:length^3 ratios were more likely to forage on moonlit nights than those with higher ratios, indicating that energy reserves were an important factor in the choice to forage while exposed to moonlight. We controlled the food offered to scorpions, but we did not control whether they actually ate, nor the scorpion size to prey size ratio. Therefore, motivation for foraging likely varied among the scorpions, though randomly with respect to fluorescence. If some fluorescent scorpions chose to seek cover while others chose to "forage" in the open, we would expect to see precisely what was observed in this experiment: reduced activity levels of fluorescent scorpions coupled with an increase in the variance of time spent in the dark caused by fluorescent scorpions choosing to spend most of their time in either the darkened or exposed habitat, with the specific choice influenced by hunger levels.

The post hoc inspection of fluorescent scorpions behavior when exposed to UV light is consistent this interpretation (with of course the caveat that it is post hoc). Fluorescent scorpions exposed to UV light exhibited a tendency to stay in one light environment that was not evident in any other treatment combination, consistent with the idea that they are making an active decision about where to spend their time in response to UV light, even if the decisions of individual scorpions differed. The reduced-fluorescence scorpions did not

exhibit this tendency. If this interpretation is correct, an experiment comparing starved to fed scorpions with and without UV present should reveal that fed scorpions seek cover from UV light while starved scorpions choose exposure to UV light, and this difference should disappear in scorpions that have had their fluorescence reduced.

Previous work on light-detection abilities of scorpions has shown UV light sensitivity in the lateral eyes (but not the median eyes; Machan 1968) and in an extra-ocular light sense localized in the metasoma (Zwicky 1968, 1970). Because the sensitivities of these senses are very similar (Zwicky 1970), we cannot at present attribute the observed changes in behavior to either one of these sensory mechanisms, and indeed it may involve both. Future experiments could attempt to determine the relative effect each of these senses has on the behavior with finer control of UV light wavelengths, and with more detailed information on the spectral sensitivities of these different mechanisms.

Machan (1968) also showed that scorpion lateral eyes have a second peak in sensitivity near the wavelength of peak fluorescence emission, which is also the region of the peak in median eye sensitivity. This dual peak in scorpion vision has suggested the possibility that scorpions possess dichromatic vision (Machan 1968; Kloock 2008). However, our results suggest another possibility. The peak in sensitivity in the UV range measured by Machan (1968) may have been caused by the eye detecting fluorescence caused by UV light, rather than by directly detecting UV light. In other words, the observed peak in sensitivity to UV light may be partially or entirely a byproduct of sensitivity to the light produced by fluorescence. If the UV sensitivity peak is actually a byproduct of fluorescence, we should see the peak in sensitivity disappear (or at least drop in amplitude) in reduced-fluorescence scorpions relative to fluorescent scorpions when the cuticle is exposed to UV light.

This study provides the first experimental evidence supporting a function for scorpion fluorescence. Further work will be necessary to link UV light detection to uses that scorpions may have for this ability in their natural habitat. Although the mechanism of detection is unclear, potentially being mediated through vision, the extra-ocular light sense or a third, as yet unknown, mechanism, the role of fluorescence in UV light detection may have implications for our understanding of fluorescence and the role of light in scorpions' sensory world.

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Social organization of the colonial spider *Leucauge* sp. in the Neotropics: vertical stratification within colonies

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Abstract. A first step toward understanding why sociality has evolved in a particular taxonomic group is to establish comparison points by studying the organization of different social systems. We examined the social organization and spatial distribution of individuals in colonies of the undescribed colonial spider *Leucauge* sp. (Araneae: Tetragnathidae). The social organization of this species was typical of a colonial species, with spiders maintaining individual territories (orb webs) within a scaffolding of shared support lines maintained by the group. Furthermore, we observed a size-dependent vertical stratification of spiders within colonies, with large spiders occupying the highest positions, followed by medium, extra-small and small individuals, a spacing pattern that was consistent across colonies of all sizes. Spiders captured and consumed prey individually and displayed territorial behaviors involving web defense. This study provides a new example of a colonial spider species that shows a distinctive within-group spatial distribution. We discuss possible reasons underlying this species' spatial arrangement in the context of social evolution.

Keywords: Aggregation, group living, orb web, sociality, spatial distribution

Knowledge about the social organization of particular species provides key insight into the mechanisms and conditions involved in the evolution of sociality. Spiders have proven to be good model systems for the study of social evolution because they encompass a large range of social phenotypes (see Avilés 1997; Uetz & Hieber 1997; Lubin & Bilde 2007 for classic and recent reviews). The few species that express social tendencies fall into two broad categories defined by individuals' level of cooperation and group structure: 'colonial' and 'cooperative' (Avilés 1997; Uetz & Hieber 1997). Colonial (or territorial permanent-social) species are generally orb-weaving spiders that spin individual webs and form permanent groups with low dispersal rates. A colonial lifestyle is characterized by the grouping of individual webs that serve as foraging or multi-purpose territories depending on the species, and which are usually maintained by single individuals. Group members engage in individual activities on their webs (e.g., foraging, brood rearing), and cooperation is usually limited to the maintenance of shared framework silk that joins the different webs (but see Fernández Campón 2007 for an example of cooperative foraging). Conversely, cooperative (or non-territorial permanent social) spiders form permanent groups on communal webs without any spatial separation between group members, and individuals cooperate in various activities such as prey capture, web maintenance and parental care. Although both social structures have evolved independently multiple times, these two organizational schemes represent distinct evolutionary pathways to sociality (Lubin & Bilde 2007).

The social organization of a group of individuals may be characterized by various attributes, such as spatial arrangement, temporal pattern, behavioral interactions and genetic relationships. The characteristics of these social attributes depend largely on the tradeoffs between the benefits and costs of communal living. In colonial spiders, benefits of group living include decreased per capita silk investment due to a shared silk framework (Uetz & Hieber 1997), increased accessibility to areas of high prey availability (e.g., open space over bodies of water) otherwise out of the reach of solitary spiders (Buskirk 1975a; Smith 1983), enhanced predator warning (Uetz et al. 2002) and increased prey capture success due to the proximity between individual webs that may cause prey to 'ricochet' from one web to the next (Uetz 1989; Whitehouse & Lubin 2005). However, coloniality also involves costs, such as increased vulnerability to predators or parasites and competition for local resources including food and web space (Buskirk 1975a, b; Uetz & Hieber 1997; Rayor & Uetz 2000).

In this study, we document the colonial structure of a recently discovered and undescribed neotropical spider, *Leucauge* sp. (referred to as *Plesiometa* sp. in Avilés et al. 2001). This orb-weaving species has previously been categorized as 'colonial' by Avilés et al. (2001), based on limited data about its social organization. To address this shortcoming, we examined the social organization of *Leucauge* sp. colonies, focusing on group composition, colony architecture and the social dynamics involved in territory maintenance and foraging. Spatial structuring within colonies may reflect a need for individuals to maximize resource acquisition and survival in a group-living situation where competition and predation pressure may impose constraints. Based on our preliminary observations suggesting a spatial arrangement of individuals within colonies, we tested the hypothesis that the distribution of *Leucauge* sp. individuals within a colony is non-random with respect to spider size, a proxy for age class.

METHODS

Study area.—We conducted this study in late August 2005 in the Jatun Sacha Biological Reserve (01°04′S, 77°36′W, elev. 400–440 m), in the Napo Province of eastern Ecuador in the

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Figure 1.—a) *Leucauge* sp. above a stream in the lowland rainforest of Ecuador: several visible orb webs (O) are joined together by framework silk (F) and anchored to the vegetation with long support lines (S). b) Adult male and c) adult female *Leucauge* sp. spider on an orb web (scale bars = 10 mm). Photo credits: a) and c) L. Avilés; b) A. Larocque.

Amazon basin. The reserve comprises 2200 ha of 70% primary and 30% secondary tropical rainforest in a transitional region between the lower Andean slopes and the Amazonian lowlands (Jatun Sacha Foundation 2009).

Study species.—The orb-weaving spider *Leucauge* sp. (Araneae: Tetragnathidae) is a territorial permanent-social species found in neotropical rainforests. This species was first characterized in Ecuador by Avilés et al. (2001) and bears significant morphological resemblance to *Leucauge argyra* (Walckenaer 1841) (= *Plesiometa argyra*: Platnick 2009). *Leucauge* sp. spiders are black with a prominent white patch on the abdomen outlined with silver bands and red coloring on their prosoma (Fig. 1b, c). They spin individual orb webs that may reach close to 1 m in diameter and are usually found in riparian habitats of the rainforest above creeks or other bodies of water inside the forest (personal observation; Avilés et al. 2001). Colonies consist of clusters of individual orb webs joined together through a framework of shared silk scaffolding that is anchored to the vegetation on the banks of a body of water with thick silk threads (Fig. 1a). Their phenology and dispersal patterns are unknown, although we have observed spiders of all age classes in August.

Data collection and analysis.—This study consisted of two parts: a population survey of *Leucauge* sp. colonies ($n = 22$) at the study site and behavioral observations of a single colony.

Population survey: We collected the following population data over two days: (1) number of spiders per colony and, for each spider therein, (2) spider body size, (3) height of the spider from the ground and (4) location within the colony. Spider body size, measured with a ruler as total body length (distance from the front of the prosoma to the tip of the abdomen), reflects both developmental stage and feeding history in spiders (Jakob et al. 1996). We grouped spiders into four size classes based on the overall distribution of observed body lengths: large ('L', average length: 11–12 mm), medium ('M', 7–9 mm), small ('S', 5–6 mm) and extra-small ('XS', 3–4 mm). L spiders were adult females and males, M spiders were sub-adults and both S and XS spiders were juveniles of various instars. We measured a spider's height from the ground as the distance from the surface of a body of water directly below a colony to the center of the spider's body. Spider location within the colony was categorized as on (1) an orb, (2) a support strand within the silk framework, (3) a dragline produced by the spider and attached to the web complex or (4) plant substrate at the periphery of a colony (usually the underside of a leaf). We collected these data on days without rain.

For analysis, we first checked the data for normality and heteroscedasticity and applied transformations where appropriate. We excluded three colonies with fewer than five spiders from the analyses (see Fig. 2). To examine differences in the distribution of spider sizes among colonies we used a log-likelihood ratio test with William's correction for small sample sizes (Sokal & Rohlf 1995). We used a logistic regression model to test the effect of colony size on spider size distributions within colonies. We assessed the relationship between a spider's size and its location within a colony using a log-likelihood ratio test with William's correction. Finally, we used a general linear model (GLM) to examine the effects of colony size and spider size on a spider's height above the ground (log-transformed), using averages for each spider size class within each colony to avoid pseudoreplication. We also assessed the relationship between colony size and the average height from the ground (log-transformed) of all spiders within a colony using a GLM and Spearman's rank correlation.

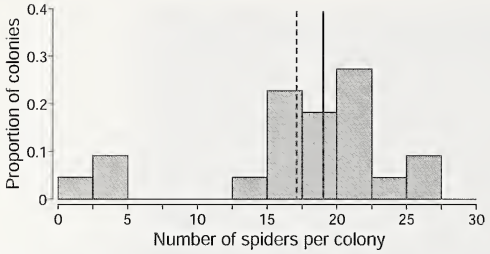

Figure 2.—Distribution of *Leucauge* sp. colony sizes (n = 22 colonies). The plain vertical line indicates the median colony size and the dashed vertical line the mean colony size.

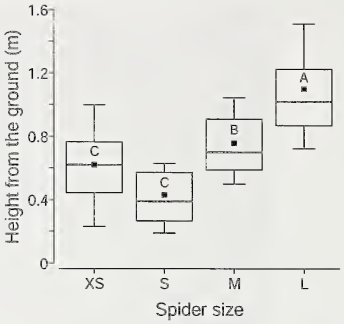

Figure 3.—Distribution of *Leucauge* sp. spiders' heights from the ground (i.e., the water surface) as a function of body size (XS = extra-small; S = small; M = medium; L = large). Boxplots show medians (thick lines), means (filled squares), 25th and 75th percentiles (bottom and top of boxes) and 10th and 90th percentiles (cap of lower and upper whiskers). Letters inside the boxes denote differences between body-size classes based on Bonferroni-adjusted pairwise contrasts (see Results).

Behavioral observations: The behavioral component of the study consisted of the observation of a single colony for 10 h per day (0700–1700 hours) on two consecutive days. Our purpose was to record foraging activities and territorial interactions among colony members. The focal colony was chosen for ease of access, median colony size and the presence of all age classes (21 adults, subadults and juveniles). It was located on a sunny tree fall over a small creek. We observed the colony continuously over 10 h, and for each individual web in the colony we recorded (1) all successful prey capture events and the identity of the spider(s) involved in a capture and (2) the number of territorial interactions and the identity of both the intruding and resident spider. We continuously observed interactions between spiders until they led to a clear outcome (e.g., stay versus retreat). To increase our sample size, we also monitored prey capture at another colony of similar size. We estimated prey size (total body length) visually and recorded the prey's taxonomic order. Prey biomass (dry weight) was calculated from total body length using insect-order specific regression models developed by Sage (1982). For analysis, we combined prey size and biomass data from both colonies.

RESULTS

Social organization and colony architecture.—Colonies ranged in size from 2–27 spiders, with a median group size of 19 (Fig. 2). Most colonies contained multiple adult females, adult males, sub-adults and juveniles. A colony typically consisted of a collection of individual orb webs arranged in a three-dimensional pattern and connected by a framework of silk forming a web complex (Fig. 1a). Orb webs were organized into multiple non-horizontal planes oriented either at the same angle or at different angles from each other (differences in orientation $< 90°$). Neighboring webs were closely arrayed and often faced similar directions (some were as close as 10 cm apart). The horizontal dimensions of a colonial web complex were usually proportional to the width and topology of the body of water above which they were placed and ranged from 0.5–3 m. Web complexes had a dense three-dimensional core with flattened edges connecting to the vegetation at the water's edge (Fig. 1a), and colony height was proportional to the number of spiders (see 'Spatial arrangement within colonies').

Web size (i.e. orb diameter) scaled positively with spider size: larger spiders occupied larger webs (personal observation). Individuals maintained individual territories (orb webs), although they were commonly seen moving between webs while travelling to other parts of the web complex, and some spiders did not own a web. When disturbed, spiders would typically flee along shared support silk threads to common retreats in the vegetation at the end of the anchor points to the substrate. Web owners regularly maintained their orb webs (i.e., as the need arose), and both spiders that owned webs and web-less spiders maintained the support silk framework. Web building was most common in the early morning and evening.

Spatial arrangement within colonies.—There was significant heterogeneity across colonies in the proportion of spiders of different size classes (large, medium, small and extra-small; G_{adj} = 78.39, P = 0.02, df = 54). However, the distribution of spider sizes across colonies was independent of colony size (χ^2 = 6.43, df = 3, P = 0.09) except that extra-small spiders tended to be more common than small ones in large colonies (χ^2 = 5.67, P = 0.02). Large- and medium-sized spiders were more likely to occupy an orb, and small and extra-small spiders were more likely to be found on the framework, a dragline or the underside of peripheral leaves (G_{adj} = 120.58, df = 9, $P < 0.0001$).

A spider's vertical position within a colony was positively correlated with its size class ($F_{3,68}$ = 22.54, $P < 0.0001$; Fig. 3). Large spiders assumed the highest positions in a colony (mean height ± SD: 1.10 ± 0.35 m, n_L = 108), followed by medium-sized spiders (0.76 ± 0.26 m, n_M = 70). Small spiders occurred closest to the bottom of the web complex (0.43 ± 0.22 m, n_S = 73) whereas extra-small spiders clustered in between medium and small spiders (0.63 ± 0.28 m, n_{XS} = 114), apparently lacking individual orb webs. Therefore, from highest to lowest, the spiders from each size class were distributed as L > M > XS > S within a colony, with adults closer to the top and juveniles closer to bottom of the web complex. Bonferroni-adjusted contrasts revealed significant

pairwise differences between each size class ($P < 0.05$) except between XS and S ($P = 0.38$; see Fig. 3). The correlation between height from the ground and spider body size held for colonies of all sizes as there was no significant interaction between spider size and colony size ($F_{3,68} = 0.94$, $P = 0.43$). Furthermore, the average height at which spiders of each size class occurred across colonies did not vary with colony size ($F_{1,68} = 2.82$, $P = 0.10$). However, the overall height from the ground of spiders in each colony increased with colony size ($F_{1,17} = 5.25$, $P = 0.03$), suggesting that colonies grow vertically. This relationship was stronger when the three smallest colonies with fewer than five spiders were included in the analysis ($r_s = 0.71$, $n = 22$, $P = 0.0002$).

Territorial behavior.—We observed 20 attempts by eight different web-less spiders to displace web-holding individuals ("attacks") on six different webs within the focal colony. Most of these attacks (16/20, 80%) took place on webs located in the center of the web complex and involved adult spiders. Responses to attacks followed an escalating pattern of agonistic behavior typically seen in colonial species (Buskirk 1975b; Hodge & Uetz 1995). Upon approach by an intruder, resident spiders positioned at the hub of the orb web would typically orient towards the intruder. The resident spider would then either contract all eight legs simultaneously, resulting in a rhythmic pulsing lasting 5–10 s that forced the intruder to halt and brace itself, or pluck the web by repeatedly jerking web radii with the front legs that also forced the intruder to brace itself (on two occasions jerks caused intruding spiders to fall out of the orb web). If intruders persisted and approached closer, the resident spider would rush out to face the intruder at the periphery of the web in a one-on-one encounter lasting from < 1 s to 3–4 s, with legs and pedipalps entangled in a blur of activity. After such an encounter, the loser would retreat a short distance and the victor would scramble to the hub of the orb. Resident spiders most often won these encounters, repelling 85% (17/20) of attackers and maintaining their ownership of a web. Spiders not occupying orbs were generally tolerant of each other as close approach and even touching was observed on framework lines of the web complex without any agonistic interactions.

Foraging behavior.—In the focal colony, we observed 23 prey capture events by 11 different spiders on 10 different orb webs. In the second colony we observed an additional 23 prey capture events. Most prey entered the web complex from the side; a few entered from the bottom. Spiders captured and consumed prey individually without cooperating. In both colonies, prey were mostly dipterans with a few hymenopterans and lepidopterans, and ranged from 1–15 mm in length (dry mass = 0.17–25.87 mg) with a majority of prey being small (median length = 2 mm; median dry mass = 0.32 mg; Fig. 4). Few prey were ≥10 mm in length (focal colony: 2/23, 8.7%; second colony: 3/23. 13.0%), but these accounted for 46.7% (focal colony) and 72.5% (second colony) of the total prey biomass. Because these data represent a small prey sampling effort, the exact shape of the distributions should be considered with caution, whereas the overall pattern is robust.

Prey capture occurred throughout the day: 13/23 (56.5%) captures took place between 0800–1200 hours and the remainder (43.5%) took place between 1300–1700 hours; no prey were captured between 1200–1300. In the focal colony, five different spiders captured one prey each and six spiders captured two to four prey each. Spiders occupying webs located in the center of a colony secured 11 out of 23 (47.8%) prey captures, and those at the periphery had 12 out of 23 (52.2%) prey captures. We once observed a spider successfully stealing a prey item captured by another spider; no other conflict over prey between spiders was observed.

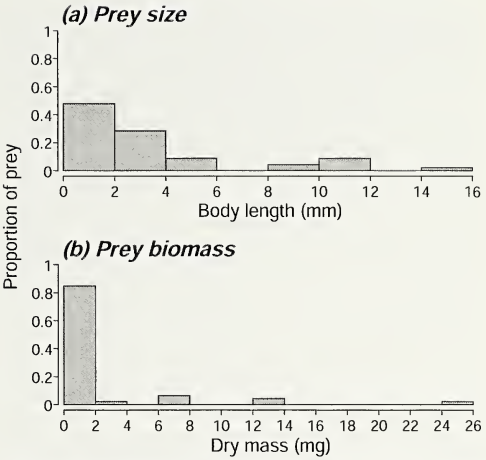

Figure 4.—Distribution of prey captured by *Leucauge* sp. spiders in terms of a) size and b) biomass.

DISCUSSION

This study presents the first empirical evidence of a colonial social organization in the recently discovered neotropical spider *Leucauge* sp. (Avilés et al. 2001). In colonies from the lowland rainforest of Ecuador, spiders maintained individual orb web territories within a framework of shared silk and engaged in individual prey capture. Our population survey showed that the spatial distribution of individuals within colonies is vertically stratified, supporting our hypothesis of a non-random spatial distribution. Colonies were vertically stratified according to spider size so that large spiders positioned themselves closest to the top, medium-sized spiders were found below large ones, and small spiders occupied webs that were closest to the bottom of the colony. Extra-small spiders occurred within the vertical range of small and medium spiders, as they usually did not own a web but instead lived as floaters in the colony's framework (i.e., an orb-less silk matrix within the colony's web complex). This non-random spatial distribution of individuals within colonies suggests that the social organization of *Leucauge* sp. follows a hierarchical arrangement, which may be explained in at least three non-mutually exclusive ways.

First, this size-dependent spatial distribution may result from environmental opportunity within a habitat. In *Leucauge* sp. colonies, larger spiders spin larger orb webs, as with other colonial (e.g. *Metabus gravidus* Pickard-Cambridge 1899 (Buskirk 1975a); *Metepeira incrassata* Pickard-Cambridge 1903 (Rayor & Uetz 2000) and usually solitary orb-weaving

species (e.g., *Cyclosa* spp. Menge 1866 (Miyashita 1997); *Leucauge mariana* (Taczanowski 1881) (Eberhard 1988); *Nephila clavipes* (Linnaeus 1767) (Higgins & Buskirk 1992)). The highest positions in a colony may better accommodate large orb webs, causing size-related variation in space occupation. Likewise, habitat parameters such as topography and the availability and orientation of web attachment points may affect spacing patterns within spider colonies. For example, in *Metabus gravidus* colonies, the average height of individual orb webs depends on the water current of the stream beneath a colony and the distance between the stream banks (Buskirk 1975a). Further research is needed to determine how the physical characteristics of habitats occupied by *Leucauge* sp. colonies affect their spatial organization.

Alternatively, the spatial stratification of individuals within *Leucauge* sp. colonies may be the result of interactions among colony members. The spatial arrangement of co-occurring spiders within a habitat is commonly thought to reflect competition between individuals for the occupancy of profitable locations (Wise 1993). Along these lines, Herberstein (1998) showed through a manipulative experiment that competition for habitat space between two co-occurring species of web-building linyphiid spiders leads to vertical stratification of species within the habitat. Likewise, competition among conspecifics may produce spatial structure within a colony. Leborgne & Pasquet (1987) showed that the spatial organization of *Zygiella x-notata* (Clerck 1757) spiders living in aggregations is density-dependent. At high densities, cohabitation between spiders of different sizes involved modulations in web size because the presence of large spiders with large webs caused smaller individuals to spin smaller webs.

Similar competitive interactions correlated with individual differences in age and size may affect spatial structuring in group-living species. In the colonial species *Metepeira incrassata*, spiders distribute themselves in a size-dependent pattern (Rayor & Uetz 1990). Large females compete for prime positions close to the core of the colony that afford the best protection from predators, whereas smaller immature spiders live closer to the edge of the web complex where both prey and predators are more common. This spatial arrangement reflects a tradeoff between the foraging and protective requirements of different age classes and results in a hierarchical distribution across different parts of the web complex based on competition for specific environmental conditions. In *Leucauge* sp. colonies, individuals may compete for the highest locations, and larger spiders may dominate due to their size advantage, just as in *M. incrassata* colonies (Rayor & Uetz 2000). To determine if the spatial arrangement of spiders within *Leucauge* sp. web complexes is based on competitive interactions, we would need to conduct field manipulations of spider size composition within colonies and environmental conditions (e.g., predation pressure) at different heights above the ground.

Why would the highest positions in a web complex be the most coveted ones? One likely explanation is based on the fact that groups of colonial spiders are commonly viewed as 'foraging societies' that form to increase individuals' foraging potentials (Whitehouse & Lubin 2005). In a foraging society, individuals may compete for locations within a colony where prey availability is higher or prey are more profitable. This may be especially true in tropical forests, where insect abundance, diversity and size vary with the height above ground, even at small spatial scales (Stork & Blackburn 1993; Basset et al. 2001). For example, Buskirk (1975a) found important spatial differences in insect species composition and abundance associated with the distance above and around streams occupied by *Metabus gravidus* spider colonies in tropical riparian habitats. Therefore, *Leucauge* sp. spiders positioned at different vertical locations within colonies may have access to different insect prey communities. In populations of *Leucauge venusta* (Walckenaer 1841) spiders from southern Mexico, the vertical distribution of webs on coffee plants is correlated with prey size and availability; large spiders build webs at an average height of 150 cm where prey are larger than at ground level, whereas small spiders build webs close to the ground where prey are smaller but more abundant (Hénaut et al. 2006). If rainforest habitats occupied by *Leucauge* sp. colonies have a similar spatial distribution of prey, large prey would be more common at the top of colonies compared to the bottom, which large adult spiders living close to the top may capture more easily than smaller subadult or juvenile spiders. Likewise, juveniles living closer to the bottom may have access to small but abundant prey.

Another possible explanation for the greater intrinsic value of high positions within a colony invokes the architectural properties of a colonial web complex. Spiders living higher up in a web complex may enjoy more architectural stability because they are less susceptible to sources of physical disturbance such as seasonal changes in water levels that may destroy webs.

Differences in the timing of web building between spiders of different sizes may also create heterogeneity in the spatial positioning of individuals. Rayor & Uetz (2000) found evidence for a sequential web-building pattern correlated with spider age and size in the colonial spider *M. incrassata*, with larger individuals securing prime web sites sooner at the expense of smaller ones. Similarly, the different positions occupied by *Leucauge* sp. spiders may depend on their age and web-building abilities. We found that individuals actively defend their webs against intruders, suggesting that they may also compete temporally to secure favorable positions. Individuals may then shift positions as they grow to progressively occupy more competitive locations. Further research is needed to examine this hypothesis in more detail.

Spatial positioning ultimately depends on compromises between the foraging, protective and structural costs and benefits procured by different locations within of a colonial web complex. For example, locations with a higher incidence of large insects may also be more exposed to predatory insects, from which larger spiders may be better protected and thus afford to live in. Conversely, small spiders may settle where the prey and predator fauna may be more suitable.

It is not known whether coloniality provides any individual fitness benefits to *Leucauge* sp. spiders, such as reduced web-building costs. In a congeneric species found in secondary forests of central Costa Rica, *Leucauge mariana*, spiders form local aggregations of adults during the dry season and tend to live solitarily the rest of the year (W. G. Eberhard, pers.

comm.; Valerio & Herrero 1977). In these aggregations, individual orbs lack the surrounding tangle lines that support the web and are solidly anchored to the substrate through shared support silk strands. Therefore, the main benefit invoked for group living in these colonies is an economy of silk (Valerio & Herrero 1977).

In summary, this study documents the colonial social organization of *Leucauge* sp. spiders. We showed that colonies follow a size-dependent spatial arrangement with a positive vertical stratification correlated with spider body size. The characterization of a spatial pattern within colonial spider groups provides further evidence that social groups are organized in specific ways to meet environmental challenges, and provides insight into the forces that shape the evolution of social systems. Future research should determine the underlying causes and mechanisms responsible for this observed spatial structure by conducting manipulative experiments and ecological studies.

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Courtship and mating behavior of the wolf spider *Schizocosa bilineata* (Araneae: Lycosidae)

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Abstract. Of all the wolf spiders (Araneae: Lycosidae), the genus *Schizocosa* Chamberlin 1904 is probably the most widely studied, and has become an established model in studies of behavior, sexual selection, and speciation. Much of the work to date involves the complex, often multimodal courtship behaviors and secondary sexual traits used by males to elicit receptivity from potential mates. *Schizocosa bilineata* (Emerton 1885) is one of those species where males possess decorative tufts of bristles on the forelegs that likely play a role in sexual selection, but little is known of male courtship behavior or its role in mate choice. In the present study, we provide the first description of visual and seismic behaviors performed by males in response to female silk and chemical cues, and examine male-female behavioral interactions in live mating trials. Males clearly recognized and responded to female chemical cues by displaying several species-specific visual signaling behaviors accompanied by seismic signals from stridulation. As these behaviors rarely occurred in the absence of female cues, we suggest they function primarily in a courtship context. In live mating trials, females typically responded to male courtship with visual receptivity behaviors, which were seen prior to mounting and copulation. While both visual and seismic signals of males are clearly implicated in courtship and mate choice, future work will be necessary to fully understand the interaction between modalities in this species. The description of behavior provided here should help resolve the relationship between male ornamentation and courtship behavior in the genus *Schizocosa*.

Keywords: Chemical signaling, multimodal communication, sexual selection

Probably the most widely studied of all the wolf spiders (Lycosidae), are members of the genus *Schizocosa* Chamberlin 1904. The genus has become an established model for exploring many aspects of evolution and speciation, multimodal communication, and sexual selection (reviewed in Uetz 2000; Uetz & Roberts 2002; Hebets & Papaj 2005; Framenau & Hebets 2007), for which studies of members of the *S. ocreata* clade (Stratton 2005) have been especially informative. The importance and utility of this genus for scientific study is due not only to the fact that most *Schizocosa* species are relatively easy to collect and maintain in the laboratory, but more importantly because males of many species possess complex, sexually selected courtship elements and secondary sexual characteristics (decorative tufts and/or pigmentation) that can be manipulated in a number of ways for study (reviews in Uetz & Roberts 2002; Hebets & Papaj 2005; Stratton 2005; Framenau & Hebets 2007). In the most recent comprehensive morphological phylogeny of the North American *Schizocosa*, Stratton (2005) divided the genus into three major clades: Clade A, containing most of the species from eastern North America as well as the well-studied *S. ocreata* clade, and the much smaller Clades B and C, containing many western and southern species. Despite extensive work on several members of this genus, there remain a number of described species for which little or no behavioral data have been collected (Stratton 2005). This is unfortunate as it prevents definitive conclusions about any correlation between male ornamentation and courtship behavior in *Schizocosa* (Stratton 2005).

Currently, courtship and mating behavior has been described for all but three of the 17 species contained within Clade A [*S. bilineata* (Emerton 1885), *S. humilis* (Banks 1892), and *S. segregata* Gertsch & Wallace 1937]. *Schizocosa bilineata* is the focus of the present study. Stratton (2005) placed *S. bilineata* as a sister taxon to *S. crassipalpata* Roewer 1951 within Clade A, but outside the *S. ocreata* clade. This placement is consistent with the more recent molecular phylogeny by Hebets and Vink (2007). While specimens of *S. bilineata* have turned up periodically in collections, species descriptions, and taxonomic studies (Montgomery 1902, 1904; Chamberlin 1908; Comstock 1912, 1940; Kaston 1948; Dondale & Redner 1978, 1990; Sierwald et al. 2005; Stratton 2005; Finkes et al. 2006; Framenau & Hebets 2007; Hebets & Vink 2007), they have otherwise received little attention. A unique opportunity to address this lack of information arose when we discovered a sizable population of *S. bilineata* on and around the campus of The Ohio State University at Newark in Newark, Ohio, USA in May 2006.

Schizocosa bilineata is a Nearctic species, thought to be widely distributed throughout the eastern part of North America, from Canada south to Georgia and Texas, and from the East coast to as far west as Kansas and Nebraska (Comstock 1940; Kaston 1948; Dondale & Redner 1990; Sierwald et al. 2005; Stratton 2005). Females of this species are light brown to yellow and cryptically colored. Males are also light brown to pale yellow (often lighter than females) but, as in several other *Schizocosa* species, have dark tufts of bristles on the tibia of their forelegs at maturity which may play a role in courtship and mate attraction. Montgomery (1903) provided the only known description of courtship and mating behavior for this species based on direct observation, in which he specified that he could find no evidence of visual courtship from males prior to mounting and copulation. Based on this finding, Kaston (1936) included *S. bilineata* in his comparative analysis of courtship behavior as an example of a species possessing secondary sexual traits but lacking visual displays (without confirming by direct observation), and this has likely

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hindered further work on the species. In the present study, we first describe visual display behaviors performed by the males during mate searching and courtship, challenging the original assessment of male courtship by Montgomery (1903). We then provide evidence of seismic communication by males, confirm several male visual behaviors that occur primarily in a courtship context in response to female chemical and multimodal cues, and describe visual receptivity behaviors shown by females in live mating trials.

METHODS

Animal collection and maintenance.—*Schizocosa bilineata* were collected in open grassy habitats along riparian zones on the campus of The Ohio State University at Newark (OSUN) (40°04.155′N, 82°26.743′W). Spiders were returned to the laboratory and housed individually in opaque, square plastic containers (150 mm × 150 mm × 50 mm, 740 ml), each with a clear lid and containing a short piece of garden hose (250 mm) for shelter. Individuals were fed two or three 10-day old crickets (*Acheta domesticus*) twice a week, and provided ad libitum access to 10 ml of fully hydrated, high molecular weight polyacrylamide gel (Watersorb®, medium crystal polymer) for water and humidity. Spiders were maintained at 24 ± 1° C with a 13:11 h light: dark photoperiod. At the conclusion of each set of experiments, spiders were euthanized by freezing and preserved in 70% ethanol. Voucher specimens are available in the collections of the corresponding author (JAR) and the Denver Museum of Nature and Science.

Male *Schizocosa* are known to respond to silk and chemical cues with courtship behavior (reviewed in Uetz & Roberts 2002; Roberts & Uetz 2004a, b; Roberts & Uetz 2005), and we followed the methods outlined in Roberts & Uetz (2005) to elicit male courtship. Specifically, cues were collected from females by placing the female on a piece of filter paper (Fisherbrand® 90 mm diam) inside a clean, glass Petri dish. Females were allowed to deposit silk, chemical cues, and excreta on the filter paper for a period of 24 h, at which time they were returned to their individual containers. Filter paper disks were then used to elicit male behavioral responses.

Experiment 1: Observation and description of male behaviors.—We collected 38 *S. bilineata* (16 males & 22 females) at OSUN on 25 May–1 June 2006 for use in the description of male behaviors. All individuals were collected as adults, and therefore we had no definitive way to determine mating status or previous experience with conspecifics before starting the experiment. We assumed, therefore, that all individuals had experience with adult conspecifics and that all had likely already mated. Mating status of males was of little concern because male *Schizocosa* are likely to mate multiply (Norton & Uetz 2005), and will display in response to silk of mated females, though at considerably reduced frequency, rate, and total duration (Norton & Uetz 2005; Roberts & Uetz 2005). We therefore felt confident that we could elicit behaviorally appropriate responses from males, even using the silk of mated females. Females were maintained until they produced (and hatched) egg sacs and/or died naturally, at which time they were preserved in 70% ethanol. Spiderlings from each egg sac were counted to obtain an average number of offspring per egg sac.

Females (n = 16) were selected randomly (here and throughout using a random digits table: Rohlf & Sokal 1969) from the 19 collected without egg sacs and were used to collect silk and chemical cues to elicit male behavior. Filter paper disks containing female cues were transferred to clear plastic containers (100 × 100 × 250 mm), and males (n = 16) were gently deposited on these disks from above. Each male was filmed for 20 min using a digital video camera (Sony, Model # DCR-HC42) for later analysis. Observations of male behavior were used only to describe basic behavioral elements for the construction of an ethogram (Table 1), and we made no attempt to determine frequency, rate, and/or duration of male display elements in this experiment. Plastic containers were cleaned between trials using lens paper and 70% ethanol to remove all chemical and silk cues from previous trials, and then allowed to air dry.

To explore seismic signals of male *S. bilineata*, we followed the recording methods of Gibson & Uetz (2008), using a randomly selected set of five males and five females from the laboratory population. Females were confined to a small area (130 × 70 mm) on a poster board substrate for 24 h to deposit cues, after which they were returned to their containers. In each recording trial, we placed the poster board substrate on a non-conductive block of carpet foam on top of a heavy table within a sound isolation chamber. An acetate ring (100 mm diam) was placed over the area containing female cues, and a male was gently placed into the apparatus from above. We utilized acetate because it is transparent, allowing direct observation of male behavior, and light enough to reduce detrimental surface loading that might interfere with seismic signal transmission. Males that began courting in response to female cues were recorded for 30 s blocks using a laser Doppler vibrometer (Polytech PI, Model # PDV-100) set to a sampling rate of 12.5 kHz, a four-channel analyzer and software set to 48 dB gain (Oros Inc., Dulles, VA, USA, Model # OR24), and a laptop computer (Dell Inspiron 4100).

Experiment 2: Male response to conspecific cues.—*Schizocosa bilineata* were hand collected as juveniles in late March and early April 2007 at OSUN to ensure that all experimental individuals were virgin at the time of the study and to control for any experience with adult conspecifics that might influence behavior (Hebets 2003). Spiders were returned to the laboratory and maintained as in Experiment 1, except that individuals were checked daily for molts to obtain an exact date of maturity. All spiders used in this experiment were between one and three weeks of maturity to maximize courtship response (Roberts & Uetz 2005).

We randomly selected male spiders from the laboratory population and placed them into one of four cue treatments (resulting in slightly unequal sample sizes) as follows: "no-cue control" where males were exposed to blank filter paper (n = 10), "male silk-cues" where males were exposed to male silk and chemical cues on filter paper (n = 8), "female silk-cues" where males were exposed to female silk and chemical cues (n = 10), or "female multi-cues" where males were exposed to female silk and chemical cues as well as any potential visual and/or seismic cues from live females corralled in the same apparatus (n = 10). Additional males and females were selected randomly from the laboratory population to serve as stimulus individuals. We collected silk, chemical cues, and excreta from stimulus individuals as in Experiment 1. In each

Table 1.—Ethogram of behaviors performed by *Schizocosa bilineata*.

Behavior	Description
Male behaviors	
Chemoexplore	Active exploratory behavior where anterior, lateral surfaces of pedipalps are brushed on the substrate in rapid succession (adapted from Tietjen 1977; Stratton & Uetz 1986)
Quick Tap	One or (rarely) both extended forelegs, is/are very quickly dropped toward the substrate from an above parallel position (in live observation often perceived as a flicker of motion), often striking the substrate; simultaneous downward motion of the distal abdomen; generally performed while Stationary, but may be produced in combination with Incremental Leg Descend or Slow Jerky Walk
Incremental Leg Descend	One or (rarely) both forelegs is/are partially or fully flexed, extended vertical to the substrate, then slowly lowered (while extended) in a series of slow, short, incremental movements; generally from a stationary position, sometimes interrupted by, or culminating in, one or more Quick Taps
Slow Jerky Walk	Slow forward locomotion characterized by short, jerky, forward leg movements; may be produced independently or in combination with chemoexploratory behavior
Female behaviors	
Settle	Female lowers body to the substrate, often with forelegs extended anteriorly
Slow Turn	Generally from a stationary position, female slowly turns body either clockwise or anticlockwise one-third to almost one full turn (also called Pivot, see Miller et al. 1998)
Shared behaviors	
Approach	Directed locomotion toward the stimulus
Groom	Legs (or pedipalps) are drawn through the chelicerae (both sexes) and/or legs are brushed together rapidly (males)
Leg Raise	One or more legs are raised above parallel with the cephalothorax and then lowered without striking the ground
Locomotion	Walking with no other behaviors expressed
Orient	Turning the body to direct the posterior median eyes toward the stimulus
Retreat	Directed movement away from the stimulus
Stationary	Motionless with no other behaviors expressed
Threat Display	Both forelegs are raised above parallel with the cephalothorax in the direction of a stimulus; often culminates in approach or lunge
Wave	One foreleg (or the first pair of legs), fully extended, raised above the cephalothorax and then lowered back to the substrate; in females this sometimes precedes Settle or Slow Turn

"female multi-cues" trial, the live stimulus female was the same individual from which the silk and chemical cues were collected, and the female was corralled within a transparent acetate ring (25 mm dia.) on the filter paper containing her own silk and chemical cues. This prevented direct contact between the male and female, but specifically allowed transmission of all other multimodal signals/cues that might play a role in courtship.

Using the same clear plastic containers (10 × 100 × 250 mm) from Experiment 1, we gently deposited males onto filter paper disks from above and filmed for 5 min using a digital video camera (Sony DCR-HC42) for later analysis. Male behavior was scored according to the ethogram developed in Experiment 1 (see Table 1). We determined the frequency (total number of bouts per 300 s trial) and total duration of male behaviors described in Table 1 using JWatcher (Version 1.0), a behavioral analysis software package freely available for download from the University of California, Los Angeles. One behavior (Quick Tap – see Table 1) was scored only for frequency, as it occurs too quickly to establish a precise duration for each bout and often occurs during bouts of other behaviors. Frequency results were square root transformed, and total duration results were log transformed for analysis using the statistical software JMP version 7 (SAS Institute, Cary, North Carolina). We analyzed results by ANOVA using the Bonferroni-adjusted critical value ($\alpha = 0.005$) in all significance tests to account for multiple comparisons (Shaffer 1995). Post hoc comparisons among treatments were conducted using Tukey-Kramer HSD tests (Zar 1999).

Experiment 3: Female receptivity and mating behavior.—Following the completion of Experiment 2, we selected males ($n = 12$) and females ($n = 12$) randomly from the laboratory population and paired them arbitrarily for mating trials. Males all had prior experience with female silk and chemical cues, but not with live females. Females had no previous (adult) experience with conspecifics. Individuals used in this experiment were between 2 and 6 wk of maturity. The translucent plastic arenas (140 × 130 × 100 mm) used in this experiment were filled to a depth of 20 mm with white sand (Quikrete, #1113) to provide a semi-natural substrate with high contrast for filming. Males and females were fed two 10-day old crickets (*Acheta domesticus*) 48 h prior to the start of experiments to standardize hunger levels, and females were then placed into the apparatus 24 h before introduction of a male to deposit silk and chemical cues. At the start of a trial, males were gently deposited into the arena in the corner most nearly opposite the location of the female. We filmed pairs from above for one hour using a video camera (Watec, model # 902H2) wired to a remote recording device (Sony Digital Videocassette Recorder, model # DSR-11) for later analysis. At the end of the recording period all individuals not in copula (or cannibalized) were returned to their individual containers. Mating pairs were allowed to separate naturally and (survivors) were then returned to individual containers.

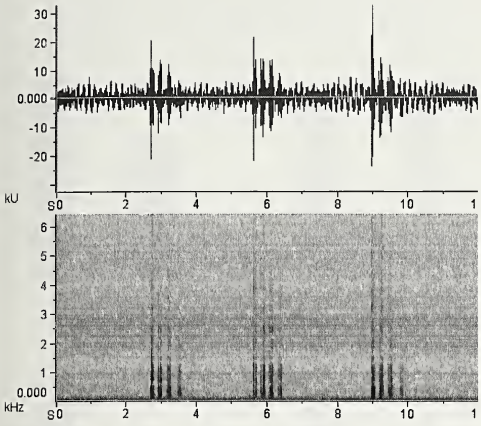

Figure 1.—Waveform and spectrogram of male *Schizocosa bilineata* seismic signaling.

RESULTS

Experiment 1: Observation and description of male behaviors.—Basic behaviors performed by male *S. bilineata* in response to female cues are similar to behaviors seen in other *Schizocosa* species (e.g., chemoexplore), but three behaviors are described which we propose as species-specific visual courtship behaviors (Incremental Leg Descend, Slow Jerky Walk, and Quick Tap). Table 1 contains a full description of all male and female behavioral elements. Further, based on recordings of seismic signals, males of this species produce distinct vibratory signals (Fig. 1). Seismic signaling bouts by male *S. bilineata* occur as short bursts of vibration, approximately one second in duration, at regular 3–5 s intervals. Each individual burst is a pulse train consisting of four pulses of stridulation, and a pulse lasts approximately 0.1 s. Though stridulatory pulses represent a sound spectrum of 1–3 kHz (with harmonics to 6 kHz), most sound energy appears to be below 1200 Hz. Unfortunately, we were only able to record brief signaling bouts of two males, so we make no attempt to further analyze aspects of the signal. Of the 22 females collected for this experiment, 20 produced (or were collected with) egg sacs. Of these twenty, 12 egg sacs (60%) successfully hatched with the number of spiderlings per egg sac ranging from two to 63 (mean = 23 ± 5.51 SE).

Experiment 2: Male response to conspecific cues.—ANOVA results for frequency and total duration of male behaviors performed in response to conspecific cues are summarized in Table 2. We did not observe some behaviors described in Experiment 1 in this experiment (Leg Raise and Retreat: Table 1), and we excluded these from analysis. Grooming and threat display did not vary significantly across treatment categories for either frequency or total duration (Table 2). Frequency and total duration of male behavior varied significantly by treatment across most other behaviors (Table 2). Orient and approach behaviors occurred only in the presence of a live female (female multi-cues), and wave occurred only in the absence of all conspecific cues (Table 2). The frequency of bouts of stationary behavior was not significantly different by treatment; however, there were significant differences by treatment for total duration (Table 2). Locomotion varied significantly across treatment categories for both frequency and total duration of behavior (Table 2), and chemoexploratory behavior was also significantly different across treatment categories with bouts occurring at higher frequency and longer duration in response to female silk cues (Table 2, Fig. 2).

Table 2.—ANOVA results for behaviors of male *Schizocosa bilineata* in response to conspecific cues in experiment 2. Key behaviors in bold.

Behavior	Frequency		Total duration	
	$F_{3,34}$	P	$F_{3,34}$	P
Approach	7.4749	0.0006*	7.0919	0.0008*
Chemoexplore	**15.7700**	**< 0.0001***	**21.2598**	**< 0.0001***
Groom	0.9787	0.4142	1.9706	0.1369
Locomotion	6.4839	0.0014*	7.7682	0.0004*
Orient	8.3509	0.0003*	6.7151	0.0011*
Quick Tap	**10.5033**	**< 0.0001***	-	-
Incremental Leg Descend	**6.0274**	**0.0021***	**10.6720**	**< 0.0001***
Slow Jerky Walk	**11.2184**	**< 0.0001***	**20.9891**	**< 0.0001***
Stationary	2.3067	0.0941	5.5349	0.0033*
Threat Display	0.7645	0.5219	0.7393	0.5360
Wave	6.2188	0.0017*	8.5837	0.0002*

* Indicates significance using Bonferroni correction ($\alpha = 0.005$)

The behaviors proposed as species-specific courtship behaviors all varied significantly by treatment for both frequency and total duration (as appropriate) of bouts (Table 2). Quick Tap was only observed in the presence of conspecific cues, but very rarely in response to male silk cues (Fig. 3). Quick Tap was considerably more frequent in response to female silk and multimodal cues, and frequency was not different between these treatments (Fig. 3). Incremental Leg Descend and Slow Jerky Walk both varied significantly by treatment for frequency and total duration of behavioral bouts (Table 2). We observed Incremental Leg Descend across all treatments, but it occurred most frequently in the presence of female cues (Fig. 4a). Bouts of Incremental Leg Descend behavior were of significantly longer duration in the female multi-cues treatment, and not significantly different across the other treatment categories (Fig. 4b). We never observed Slow Jerky Walk in response to male cues and only very rarely in the no-cue control treatment (Fig. 5a). Neither frequency nor total duration of Slow Jerky Walk was different between the female silk-cues or multi-cues treatments (Fig. 5), but both frequency and total duration were significantly higher than in the no-cue control or male silk-cue treatments (Fig. 5).

Experiment 3: Female receptivity and mating behavior.—Males exhibited chemoexploratory and courtship behaviors in all but one trial, which was excluded from further analysis, since both the male and the female remained stationary for the entire 1 h trial period. Mean latency to begin chemoexploratory behavior in the remaining trials was 7.2 s (± 2.84 SE, n = 11), and mean latency to begin courtship (defined as first instance of Quick Tap, Incremental Leg Descend, or Slow Jerky Walk) was 34.5 s (± 5.00 SE, n = 11). Female receptivity

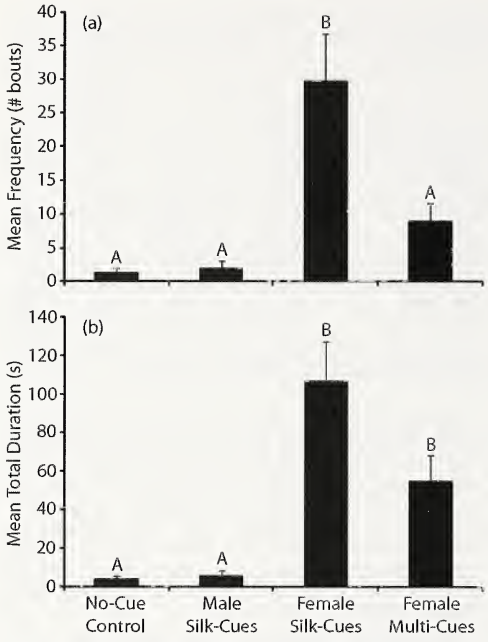

Figure 2.—Mean + SE a) frequency and b) total duration of bouts of Chemoexplore behavior for male *Schizocosa bilineata* exposed to blank control, conspecific silk cues, or multimodal female cues. Shared letters above the bars indicate no significant difference between treatment categories by Tukey-Kramer post-hoc analysis ($\alpha = 0.05$).

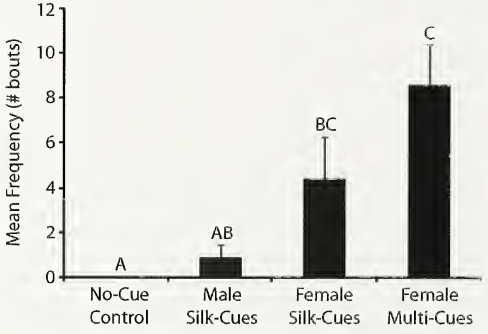

Figure 3.—Mean + SE frequency of bouts of Quick Tap behavior for male *Schizocosa bilineata* exposed to blank control, conspecific silk cues, or multimodal female cues. Significant differences for post-hoc analysis indicated as in Fig. 2.

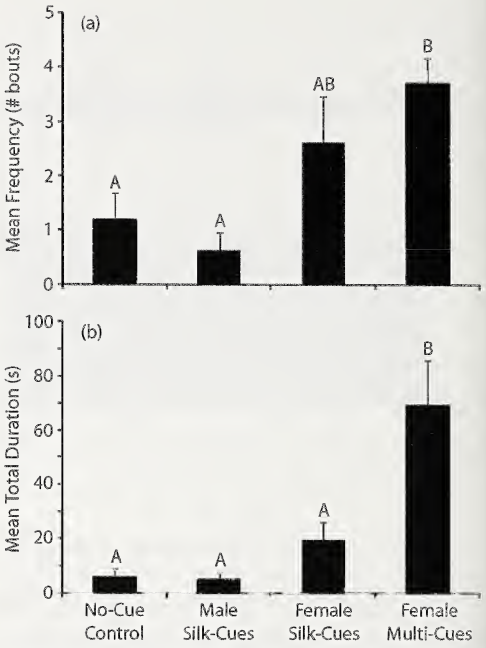

Figure 4.—Mean + SE a) frequency and b) total duration of bouts of Incremental Leg Descend behavior for male *Schizocosa bilineata* exposed to blank control, conspecific silk cues, or multimodal female cues. Significant differences for post-hoc analysis indicated as in Fig. 2.

behaviors were typical of other *Schizocosa* (summarized in Table 1) and were observed in 8 of 11 trials (72.7%). We observed mounting and copulation in 5 of 11 trials (45.5%) and mean latency to copulate in these trials was 1402.8 s (± 559.2 SE, $n = 5$). In all cases, males initiated courtship prior to attempting to mount, and females adopted a Settle position prior to mounting by the male. Four of the five females performed at least one Slow Turn prior to Settle. Males mounted females from the anterior or anterior lateral position, and copulation position was of the normal type for Lycosidae with male above on the female dorsum and facing the female posterior (Foelix 1996). We observed two instances of sexual cannibalism by females out of 11 mating trials (18.2%), one pre-copulatory and one post-copulatory.

DISCUSSION

In the Lycosidae, ornamentation of male forelegs (e.g., tufts of bristles, pigmentation) is generally associated with active leg-waving displays that play a role in visual communication. This seems especially true within the genus *Schizocosa* (Hebets & Uetz 2000; Stratton 2005; Framenau & Hebets 2007), but a few species remain within the genus for which little or no behavioral data exist (Stratton 2005). Unfortunately,

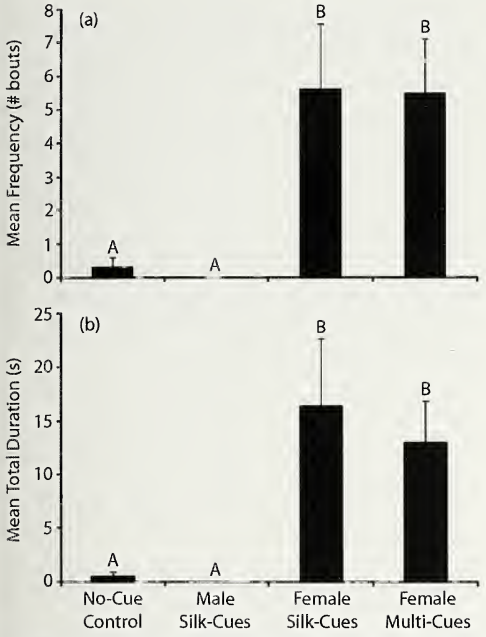

Figure 5.—Mean + SE a) frequency and b) total duration of bouts of Slow Jerky Walk behavior for male *Schizocosa bilineata* exposed to blank control, conspecific silk cues, or multimodal female cues. Significant differences for post-hoc analysis indicated as in Fig. 2.

this 'missing data' has hindered any thorough phylogeny-based exploration of the correlation between leg decoration/ornamentation and visual display behavior (Stratton 2005). The work presented here represents the first comprehensive analysis of courtship and mating behavior for *Schizocosa bilineata*, a species whose males possess leg decoration but for which little behavioral work has been done. Results clearly indicate the presence of visual display elements during male mate searching and courtship (Table 1), and refute earlier assertions by Montgomery (1903) that males of this species do not exhibit discernable visual courtship. This is not entirely surprising, as a careful review of methods reveals that the assertion is based on a single, successful male/female pairing (Montgomery 1903). In fact, three visual display behaviors (Quick Tap, Incremental Leg Descend, and Slow Jerky Walk) are described here for *S. bilineata* males and, as all three were expressed predominantly in the presence of conspecific female cues and prior to copulation in mating trials, any or all could play a role in mate choice.

Of the three male visual display behaviors, Quick Tap seems least likely to play a role in visual communication. During the real-time video analysis of male behaviors, we observed Quick Taps only as a 'flicker' of motion. This probably corresponds to the "quiver" of leg motion described by Montgomery (1903). Frame-by-frame analysis of bouts of this behavior demonstrate that each bout is conducted within three video frames at the NTSC video standard of 29.97 frames per second (corresponding to an approximate bout length of 0.1 s). Considering the visual system characteristics of wolf spiders, which have flicker fusion rates similar to humans (Land 1985; Uetz 2000), at this speed it seems likely that the behavior would serve as an attention signal or driver of seismic signals, but not function effectively as a courtship signal in and of itself.

The other two display behaviors, Incremental Leg Descend and Slow Jerky Walk, seem more promising for a role in mate choice. These behaviors are similar to behaviors in other *Schizocosa* species that have been demonstrated to be important in female mate choice. In particular, Incremental Leg Descend resembles the "Extension" behavior described for *S. crassipes* (Miller et al. 1998) and Slow Jerky Walk, the "Jerky Walk" behavior described for *S. ocreata* (Stratton & Uetz 1983, 1986). We stress, however, that the behaviors seen in *S. bilineata* are distinctly different from these other behaviors. In Incremental Leg Descend, the extended leg is slowly and incrementally lowered (in a series of pauses) to the substrate (never quickly tapped). Slow Jerky Walk is not only slower than Jerky Walk, but also lacks the distinctive cheliceral strikes and leg taps characteristic of bouts of *S. ocreata* courtship.

The assertion of a role for these behaviors in sexual selection, however, is speculative at present, despite the coincidental production of these behaviors immediately prior to copulation and in response to female cues. Additional work will be necessary to explore the actual function of the display traits in conspecific interactions. Kaston (1936) raised an important point concerning sexual traits and display behaviors (even if it was based on the faulty assumption of no visual display in *S. bilineata*). He emphasized that possession of such traits and behaviors does not necessarily mean that said characteristics are actually important for or directly involved in mate choice. This point is especially important concerning the recent work by Hebets (2008) where she demonstrates that although male *S. stridulans* Stratton 1991 produce a visual signal, only simultaneously produced seismic signals are important for female choice. We made no attempt to isolate signaling modalities (visual/seismic) in mating trials and as such, we are not able to determine whether visual or seismic cues are of greater or equal importance in this species.

We can, however, draw some important conclusions for males of this species. Clearly, as in other *Schizocosa* species, females signal to males using chemical signals associated with silk (reviewed in Roberts & Uetz 2004a, b; Roberts & Uetz 2005), and signals from chemical cues are lacking in males (Figs. 2–5). Although only rarely performed in the absence of silk and chemical cues, Slow Jerky Walk was never performed in the presence of male silk cues (Fig. 5), and thus may offer evidence for a male inhibitory chemical as suggested by Ayyagari &Tietjen (1987). Male *S. bilineata* recognize and respond to chemical cues alone with species-specific courtship behavior (Figs. 3–5), and perform bouts of one behavior (Incremental Leg Descend) for a significantly longer duration in response to live females (Fig. 4b). This suggests that males alter their behavior in response to some behavioral feedback from females, though aside from visual receptivity behavior

and chemical signals, we did not find evidence of other signaling by females. The significant increase in frequency of Quick Taps in response to female multimodal cues further supports this suggestion. Females, whether responding to visual, seismic, of multimodal male cues, do respond to male courtship with typical receptivity behaviors. These behaviors precede mounting and copulation, and males must recognize female receptivity behaviors and respond accordingly.

It is unfortunate that we were unable to fully describe male seismic signals in our study. There is a good chance that these signals play a critical role in courtship and mate choice in this species (Stratton 2005), maybe more so than visual signals alone (Hebets 2008). Future work will be necessary to fully understand the interaction between visual and seismic modalities, but both are likely important and our description of behavior in this species should help resolve the relationship between male ornamentation and courtship behavior in the genus *Schizocosa*.

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A new species of *Santinezia* (Opiliones: Cranaidae) from Panama

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Abstract. A new species, *Santinezia noctiscansor*, most similar to members of the *S. festae* group, is described from central Panama; this species is the only member of the genus that occurs in Central America. Our examinations of adults and nymphs collected from Coclé and Panamá Provinces revealed that males are sexually mature as penultimate nymphs. The subadult strongly resembles the adult with respect to coloration, scutal outline, armature of femora III–IV, and penis morphology, but differs in having fewer tarsomeres on each leg, a smaller body size (scutal length and width), and a much smaller tubercle on the ventral surface of coxa IV. Natural history observations are provided for specimens collected from the field site in Coclé Province.

Keywords: Harvestman, Laniatores, natural history, Neotropics

In the catalogue of the Laniatores of the New World, Kury (2003) listed only three species of cranaids (all members of the subfamily Cranainae) occurring in Central America: *Comboyus alblineatus* Roewer 1943 and *Phareicranaus magnus* (Roewer 1932) from Panama, and *P. ornatus* Roewer 1932 from Costa Rica and Panama. In Pinto-da-Rocha & Kury (2003), *P. magnus* was transferred to *Neocranaus*. In a brief review of the geographic distribution of the Cranaidae, Pinto-da-Rocha & Kury (2007) stated, but did not specify, that only two species in the family occur in Central America (Panama and Costa Rica). Given that *C. albilineatus* was not examined by Pinto-da-Rocha & Kury (2003), it seems likely that this species was overlooked in the later review.

In this study, we describe *Santinezia noctiscansor* based upon examinations of adult and subadult specimens collected from two sites in Panama. The genus *Santinezia* consists of 21 species of medium to large harvestmen (scutal length: 6–16 mm) that occur primarily in northern South America (Pinto-da-Rocha & Kury 2003, 2007). Males possess a large tubercle on the ventral surface of coxa IV, a feature that represents the most reliable character used for distinguishing between members of the genera *Santinezia* and *Phareicranaus* (Pinto-da-Rocha & Kury 2003). In comparison to adult females, cranaid males have more pronounced armature on leg IV (especially the femur, but also the tibia in several species) and somewhat enlarged chelicerae (Pinto-da-Rocha & Kury 2007). During postembryonic development, the sexually dimorphic femur IV is observable in the antepenultimate nymph (Townsend et al. 2009). Presently, three species groups (*curvipes*, *festae*, and *gigantea*) are distinguished on the bases of the armature on femur IV and tibia IV, the position of the ventral tubercle on coxa IV, and penis morphology (Pinto-da-Rocha & Kury 2003). Little is known about the natural history of these harvestmen. On the Caribbean island of Trinidad, adult *S. serratotibialis* (a member of the *curvipes* group) climb vegetation after dusk (Townsend et al. 2008a), occupy diurnal shelters within rotting logs and palm frond sheaths (Townsend et al. 2008a), exhibit parental care through the guarding of eggs (Machado & Warfel 2006) and nymphs (Townsend et al. 2009), and are infrequently parasitized by larval erythraeid mites (Townsend et al. 2008b).

METHODS

The adult male holotype and subadult male paratype of *Santinezia noctiscansor* were collected from montane rainforests in Coclé Province near the village of El Cope and are deposited in the American Museum of Natural History (AMNH). We examined an adult male paratype and three subadult paratypes of *S. noctiscansor* from the collections of the Museo de Invertebrados G.B. Fairchild (MIUP) at the Universidad de Panama. All specimens were observed and photographed in 70% ethanol with a digital Leica EZ 4D stereomicroscope. We took measurements with the aid of an image capturing system.

Because the taxonomic literature for the Laniatores is rich with potentially ambiguous terms for macroscopic cuticular structures (e.g., spines, tubercles, and apophyses), collectively referred to as "macrosculpture" (Acosta et al. 2007), we employed the terminology suggested by Acosta et al. (2007) with regard to spines (structures that insert into sockets) and tubercles (small, blunt projections that may or may not bear setae). However, we refer to larger structures as "spiniform tubercles" rather than "apophyses" (Acosta et al. 2007) or "spines" (e.g., Goodnight & Goodnight 1947).

For comparative purposes, we examined the female holotype of *Phareicranaus ornatus* Roewer 1932 (RII/ 2597/ 68-42) from Senckenberg Museum, Frankfurt, Germany (SMF) as well as multiple adult and nymphal specimens of *Santinezia serratotibialis* Roewer 1932 from AMNH.

KEY TO THE CRANAIDAE OF CENTRAL AMERICA

1. Only second free tergite with a pair of median tubercles; sulci I–II with conspicuous white stripes; femur IV of male armed with a large basal pair of spiniform tubercles; tarsus II with 28 segments . . . . . *Comboyus albilineatus* Roewer 1943 (Panama)
   Second and third free tergites with a median pair of tubercles; sulci I–II without conspicuous stripes; femur IV of male not armed with large, basal, spiniform tubercles on the prolateral and retrolateral surfaces; tarsus II with less than 20 segments 2

2. Coxa IV of male armed ventrally with large, median tubercle tarsus I with 9 segments *Santinezia noctiscansor* new species (Panama) .....
Coxa IV of male ventrally unarmed; tarsus I with less than 9 tarsomeres 3
3. Leg II greater than 50 mm; tarsal formula 8:17:7:7 (Roewer 1932) or 7:11–12:7:7 (Pinto-daRocha and Kury 2003) .....
..... *Neocranaus magnus* (Roewer 1932) (Panama)
Leg II less than 50 mm; tarsal formula 8:13–14:9:10 ..... *Phareicranaus ornatus* Roewer 1932 (Costa Rica)

SYSTEMATICS

Family Cranaidae Roewer 1913
Santinezia Roewer 1923

Inezia Roewer 1913:392 (preoccupied by *Inezia* Cherrie 1909); Mello-Leitão 1926:39; Mello-Leitão 1932:113 (type species *Inezia gigantea* Roewer 1913, by monotypy).

Santinezia Roewer 1923:553 (replacement name); Mello-Leitão 1932:122; Roewer 1932:289; Mello-Leitão 1935:96; Kästner 1937:389; Soares & Soares 1948:616; Roewer 1963:69; González-Sponga 1989:59 (type species *Inezia gigantea* Roewer 1913); Pinto-da-Rocha & Kury 2003:181; Kury 2003:97.

Niebla Roewer 1925:27; Roewer 1932:348; Soares & Soares 1948:610 (type species *Niebla festae* Roewer 1925, by monotypy); Synonymy established by Pinto-da-Rocha & Kury 2003:181.

Chondrocranaus Roewer 1932:341; Soares & Soares 1948:592 (type species *Chondrocranaus scriptus* Roewer 1932, by monotypy). Synonymy established by Pinto-da-Rocha & Kury 2003:181.

Macuchichola Mello-Leitão 1943:4; Soares & Soares 1948:606 (type species *Macuchicola arthrocentrica* Mello-Leitão 1943, by original designation. Synonymy established by Pinto-da-Rocha & Kury 2003:181.

Carvalholeptes H. Soares 1970:330 (type species *Carvalholeptes singularis* H. Soares 1970, by original designation). Synonymy established by Pinto-da-Rocha & Kury 2003:181.

Santinezia noctiscansor new species
(Figs. 1–7)

Type material.—PANAMA: *Coclé Province*: Holotype male, Parque Nacional General Division Omar Torrijos H., El Cope, 08°49.2′80″N, 80° 5′45.7″W, 23–28 February 2007, collected by hand along hiking trails at night in montane rainforest by V. Townsend, A. Savitzky, and J. Ray (AMNH). Paratypes: 1 subadult male, same location (AMNH); 1 adult male, Carretera El Llano Cartí, Est. Burbayar, Panamá Province (MIUP: no coordinates available); 2 subadult males, 1 subadult female, same location, 9–21 July 2007, R.J. Miranda (MIUP).

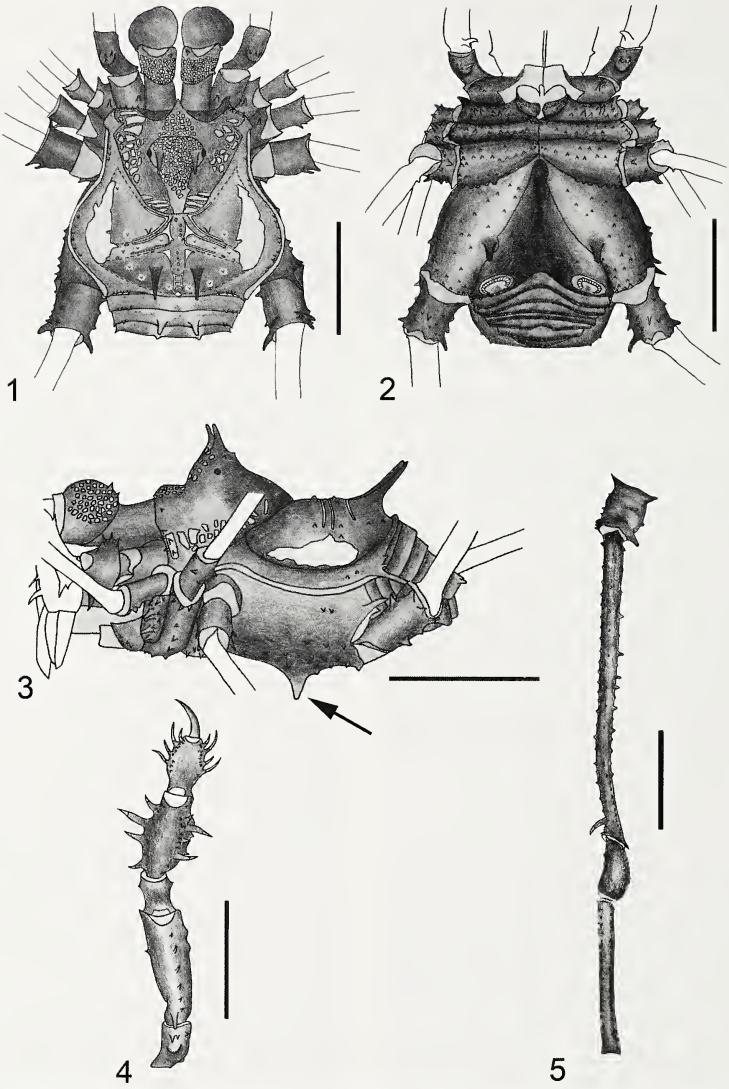
Etymology.—The name of this species is based on the Latin words *noctis* for "night" and *scansor* for "climber." It is a noun in apposition. This name refers to field observations of behavior in which several individuals (adults and nymphs) were observed climbing tree trunks up to heights of 1–2 m above the ground after dusk.

Diagnosis.—Large, ventral tubercle on coxa IV located on middle region; rows of subequal tubercles on prolateral and retrolateral surfaces of male femur IV, with retrolateral tubercles slightly larger than prolateral tubercles; femur IV with three distal spiniform tubercles, largest is prolateral, other tubercles ventral; male tibia IV straight and without 8–12 spiniform tubercles on proximal half; stylus without subdistal pointed apophyses. Superficially, this species resembles *Phareicranaus ornatus* with respect to scutal outline, dorsal pattern, general penis morphology, and the armature of male femora III–IV. However, *Santinezia noctiscansor* differs from *P. ornatus* in having a prominent ventral tubercle on male coxae IV (the major character used to distinguish between *Phareicranaus* and *Santinezia*). In addition, *Santinezia noctiscansor* differs from *P. ornatus* with respect to body size, the distribution and relative sizes of spines on the mesal surface of the tibia of the pedipalp, and tarsal formula. With respect to genital morphology, the penis of *S. noctiscansor* has a ventral plate with 3 distal, curved setae and the glans lacks a dorsal process. In contrast, the penis of *P. ornatus* has 4 distal curved setae and the glans features a dorsal process (Pinto-da-Rocha & Kury 2003). *Santinezia noctiscansor* should be considered a member of the *festae* group (Pinto-da-Rocha & Kury 2003) and represents the only known member of this genus that occurs in Panama and Central America. In addition to the position of the large, ventral tubercle on coxa IV in the male, *S. noctiscansor* also shares similar patterns of armature on trochanter III and the femur of the pedipalp with members of the *festae* group (Pinto-da-Rocha & Kury 2003). However, in contrast to other species in this group, *S. noctiscansor* exhibits distinctive morphology with respect to the armature of femur IV of the male. In addition, this species differs from *S. arthrocentrica* (Mello-Leitão 1943) in the morphology of the stylus and the armature of coxa and tibia IV and differs from *S. festae* (Roewer 1925) with respect to color pattern and the distribution of tubercles on the carapace.

Description.—*Male (holotype):* Measurements (mm): Dorsal scutum length 9.32; width 10.07; cephalothorax length 5.12; width 6.93; leg segments (Table 1). Dorsal scutum (Fig. 1): anterior border with a median projection between the chelicerae and a lateral row of 6–7 tubercles on each side.

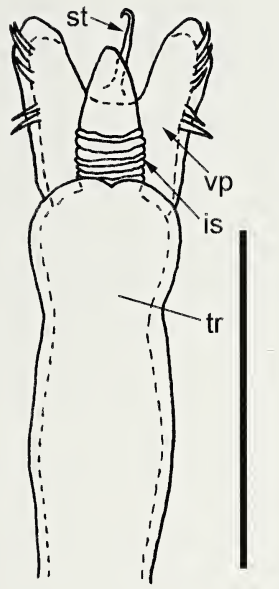
Eye mound with two large, divergent, spiniform tubercles and two smaller granular tubercles on each side, posterior to the larger tubercles.

Carapace smooth. Lateral margin of scutum with 1–3 tubercles adjacent to area I and 8–9 tubercles adjacent to areas II–III. Area I with a median pair of larger tubercles and one lateral smaller seta-bearing tubercle on each side; area II with transverse row of seta-bearing tubercles; area III with a median pair of large, spiniform tubercles and three smaller seta-bearing tubercles on each side; area IV smooth; posterior border with three lateral seta-bearing tubercles on each side. Free tergite I with two lateral tubercles on each side; II and III with median pair of larger tubercles, with median tubercles on the second free tergite larger than those on the third. Free tergite II with two lateral tubercles on each side; free tergite III with a single lateral tubercle on each side. Anal operculum with several scattered seta-bearing tubercles.



Figures 1–5.—*Santinezia noctiscansor*, adult male holotype: 1. Habitus, dorsal view; 2. Habitus, ventral view; 3. Habitus, lateral view, arrow indicates position of large, ventral spiniform tubercle on coxa IV; 4. Pedipalpus, left, ventral view; 5. Trochanter-tibia of Leg IV, left, dorsal view. Scale bars = 5 mm.

Venter (Fig. 2): Coxa I with scattered arrangement of four larger tubercles and 8–12 smaller tubercles; coxa II with median row of six tubercles, two apical tubercles, four anterior tubercles, and 4–5 posterior tubercles; coxa III with median row of 9–10 tubercles, three anterior tubercles, five posterior tubercles; coxa IV with one stout, larger tubercle covered with many scattered setae near mid-ventral portion (Fig. 3) and an additional 24–30 scattered smaller tubercles. All coxal



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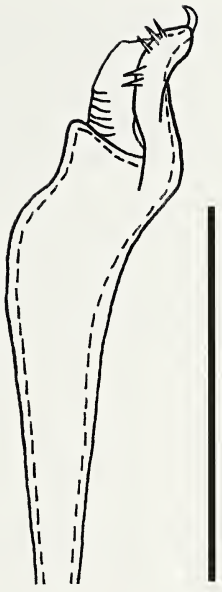

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Figures 6, 7.—*Santinezia noctiscansor*, adult male holotype, penis. 6. Dorsal view, is = inflatable sac of glans, st = stylus, tr = truncus, vp = ventral plate; 7. Lateral view. Scale bars = 0.5 mm.

tubercles bear setae. Stigmatic area and free sternites with few, scattered seta-bearing tubercles.

Chelicerae: Basichelicerite with five tubercles; hand with two frontal tubercles; fixed finger with four teeth; moveable finger with four teeth.

Table 1.—Length of the leg segments for adult (holotype) and subadult (paratype from El Cope) males of *Santinezia noctiscansor*. All measurements are in mm.

Leg Segment	Leg I	Leg II	Leg III	Leg IV
Adult male				
Trochanter	1.02	1.33	1.42	2.28
Femur	6.85	14.78	11.45	16.06
Patella	1.55	2.26	2.64	3.19
Tibia	4.05	10.57	6.51	8.40
Metatarsus	7.95	13.35	10.81	14.89
Tarsus	3.34	8.45	5.34	6.17
Total length	24.76	50.74	38.17	50.99
Subadult male				
Trochanter	0.82	1.28	1.52	2.14
Femur	6.22	13.14	10.79	13.96
Patella	1.31	1.86	2.40	2.73
Tibia	3.71	9.44	6.04	7.80
Metatarsus	6.92	12.16	9.81	13.61
Tarsus	2.95	7.83	4.84	5.44
Total length	21.93	45.71	35.40	45.68

Pedipalpus (Fig. 4): Trochanter length: 1.61 mm; femur length: 4.53 mm; patella length: 2.03 mm; tibia length: 3.69 mm; tarsus length: 4.39 mm; total length: 16.25 mm. Coxa with one ventral tubercle. Trochanter with two ventral and two dorsal tubercles. Femur with ventral row of seven tubercles, retrolateral row of five tubercles, and dorsal row of seven tubercles (most apical tubercle is larger and spiniform). Patella granular with scattered setae. Tibia dorsally granular, ventrally with four ectal (iIii) and four mesal (iIii) spines; tarsus dorsally smooth and ventrally with four ectal (iIii) and four mesal (iIii) spines.

Legs: Coxae I–II each with one large dorsal tubercle; coxa III smooth; coxa IV with 4–5 latero-dorsal tubercles and one large spiniform apical tubercle. Trochanter I dorsally smooth and ventrally with one prolateral, one median, and 1–2 retrolateral seta-bearing tubercles; trochanter II with one dorsal, three prolateral, one ventral and three retrolateral seta-bearing tubercles; trochanter III dorsally smooth and ventrally with three prolateral, 3–4 median and three retrolateral seta-bearing tubercles, apical retrolateral tubercle is largest; trochanter IV dorsally smooth and ventrally with three prolateral, 5–6 median, and three retrolateral seta-bearing tubercles; the apical prolateral and retrolateral tubercles are larger. Femora I–IV granular with organized rows of setae; femora III–IV with prominent tubercles organized into rows with tubercles on femur IV larger than those on III; femur III basally and with one larger dorsal prolateral and one dorsal

retrolateral tubercle and apically with two larger distal retrolateral tubercles; femur IV (Fig. 5) with three larger distal spiniform tubercles on ventral surface, one prolateral and two retrolateral; all three tubercles curved; dorsal row of tubercles with alternating larger and smaller tubercles; tubercles on the retrolateral and prolateral rows largest basally decreasing in size distally. Patellae I–IV granular. Tibiae I–IV granular. Tarsal formula: 9:16:10:11–12, distitarsi I–II with 3 segments.

Male genitalia (Figs. 6, 7): Ventral plate subrectangular, deeply cleft, distal corners without flange. Two groups of setae: two straight latero-basal and three curved latero-apical. Glans without dorsal process, but with inflatable sac with many similar folds arranged in a stack. Stylus smooth, slightly curved. Apex bent, without stylar apophysis.

Color: Body dark reddish brown and legs dark brown to black. Eye mound and median region of carapace lighter brown than rest of carapace. Large yellow spots occur on margin of abdominal scutum adjacent to areas I–III. Median borders of abdominal scutal areas partially outlined by yellow lines (Fig. 1). Median tubercles on areas I–III brown. Posterior borders of free tergites II–III outlined in yellow. Tubercles on second free tergite yellow. Venter dark brown. Chelicerae mottled, darker than eye mound, but lighter than carapace and legs.

Subadult male paratype: Measurements (mm): Dorsal scute length 7.78; width 8.82; cephalothorax length 4.16; width 6.09; leg segments (Table 1). Dorsal scutum: same as adult holotype. Venter (Fig. 2): same as adult holotype with the exception that the stout, larger tubercle on the ventral surface of coxa IV is less than half the overall size as that of the adult holotype. Chelicerae: same as adult holotype. Pedipalpus: Trochanter length: 1.28 mm; femur length: 3.87 mm; patella length: 1.95 mm; tibia length: 2.90 mm; tarsus length: 4.24 mm; total length: 14.24 mm. Legs: same as adult holotype except tarsal formula: 8:15:9:10. Male genitalia (Figs. 5, 6): same as adult holotype. Color: same as adult holotype.

Distribution.—This species is known from specimens collected from forests in the central Panamanian provinces of Coclé and Panamá, areas west of the Canal Zone.

Habitat.—The adult male holotype and the subadult male paratype from El Coclé were collected from the external surfaces of trunks and moss-covered buttresses of medium to large trees (0.5–1.5 m in diameter) along hiking trails in a moderately sloping montane rainforest. Specimens were collected after dark between 2100–2300 h during moderate periods of rainfall. No information regarding habitat was available for the MIUP specimens collected from Panamá Province.

Remarks.—During our sampling at the El Coclé field site, we collected adults, subadults, and three other distinct groups of nymphs (based on size and coloration) at the end of February, which corresponds to the early part of the dry season in central Panama. Due to the elevation, the field site was relatively moist and it also rained briefly each evening. The presence of multiple instars in the population indicate that *S. noctiscansor* is probably sexually active over an extended period of time at this location and that reproduction begins during the later part of the wet season or perhaps earlier. The collection of sexually mature subadults indicates that cranaids share the novel life history pattern exhibited by other members of the Grassatores, in which there are two instars, the penultimate nymph and adult, in the adult phase (Gnaspini et al. 2004).

The similarities and differences that we observed in the morphology of the subadult and adult male also raise interesting questions concerning the reliability of the identifications of cranaids in regions in which *Santinezia* species are believed to be syntopic with those of *Phareicranaus*. The most useful character for distinguishing between these genera is the presence of a prominent ventral tubercle on coxa IV of the male (Pinto-da-Rocha & Kury 2003). It is our opinion that subadult male *Santinezia* probably have, at least occasionally, been mistaken for adult male *Phareicranaus* due to the inconspicuous nature of the ventral tubercle on coxa IV during the penultimate nymph stage.

In comparing the adult male holotype (El Coclé Province) and adult male paratype (Panamá Province), we noticed several asymmetries in the holotype that were not present in the paratype. For example, in the holotype, there is a paracheliceral projection only on the right side of the anterior scutal margin (Fig. 1). In the paratype, this projection is absent and the two sides are symmetrical. Similarly, in the holotype, the left side had a greater number of tubercles than the right with respect to the abdominal scutal areas and the ventral surfaces of the coxae. In the paratype, the tubercles on each side were equivalent in number or differed by only one. The subadult paratypes were also symmetrical with respect to the anterior scutal margin and the distribution of tubercles.

In the field we did not observe any instances of feeding or predation; however, we found that several individuals were parasitized externally by larval mites. In the living condition these mites are orange to red, but when preserved, they quickly turn white (within a few weeks when stored in ethanol). We observed two distinct sizes of these mites on the specimens from El Coclé, which probably represent different species of parasites. Attachment sites for mites included the dorsal scutum, ventral surfaces of coxae and free tergites. The holotype had a small mite attached to the ventral surface of the first coxa, whereas the subadult paratype had two large mites attached to the dorsal scutum near the posterior margin of area III. The intensity of infestation was generally 1–2 mites per host.

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Natural history of the Iberian solifuge *Gluvia dorsalis* (Solifuges: Daesiidae)

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Abstract. In this paper we present a detailed study of the natural history of *Gluvia dorsalis* (Latreille 1817), a representative of the family Daesiidae, the only solifuge species known to occur in southwestern Europe. We studied its distribution, habitat preference, circadian activity, seasonal occurrence, burrowing, predatory and post-mating behavior, prey, fecundity, ontogenesis, and sexual dimorphism. *Gluvia dorsalis* occurs in lowlands across the entire Iberian Peninsula, preferring grassland or similar open-ground habitats with little summer rain. According to pitfall trap data, the species was active on the surface from May until the beginning of November. It is a nocturnal epigean predator, feeding principally on ants and spiders. However, under laboratory conditions, specimens captured and consumed a variety of arthropods. *G. dorsalis* seems to hide in underground burrows only when molting, overwintering, or laying eggs. Reproduction occurred in early summer, and females usually produced a single egg clutch containing, on average, 84 eggs, and died soon after. Our results indicate that the *G. dorsalis* is a biennial species. There was sexual dimorphism in several morphological structures that might be used for sex matching in juvenile instars.

Keywords: Camel-spider, activity, prey, reproduction, sexual dimorphism

Solifuges are one of the most important predators of arid environments (e.g., Polis & McCormick 1986; Cloudsley-Thompson 1977; Punzo 1997). Despite being locally very abundant, their natural history remains largely enigmatic, as researchers have investigated only a very few species so far. Out of 12 families and slightly more than 1,000 solifuge species currently recognized (Harvey 2003), scientists have performed a thorough natural history studies on only eight species in three families: four eremobatid (e.g., Muma 1966a, 1967; Punzo 1997, 1998a); three galeodid (Heymons 1902; Cloudsley-Thompson 1961a, b; Junqua 1966; Hrušková-Martišová et al. 2007); and one solpugid species (Wharton 1987). Biologists have studied only particular aspects of behavior, such as prey and predatory behavior (e.g., Dean & Milton 1991), reproductive behavior (Perreti & Willemart 2007), or burrowing behavior (Gore & Cushing 1980). Yet, even these data are largely fragmented. With the exception of three species (Junqua 1966; Muma 1966a; Punzo 1998a), the postembryonic development or life cycle of solifuges is virtually unknown. Only Punzo (1998a) documents the number of instars, duration of intermolt intervals, and lifespan in a single species.

Solifuges are restricted to arid regions of the world with the exception of Australia, where they do not occur. In Europe, 18 species from 4 families have been found so far (Harvey 2003). The majority of the species occur in the eastern Mediterranean, but a single species, *Gluvia dorsalis* (Latreille 1817) (Daesiidae), is endemic to the Iberian Peninsula (Fig. 1). This species was originally only described from Spain, but later collectors found it in different places across the Iberian Peninsula (Pablos 1967; de Matos 1978; Schenker 1980; Grosso-Silva 1998).

Our aim in this study is to provide a detailed natural history account of *G. dorsalis*, found to be locally quite abundant, particularly in southern Portugal. We know of no other natural history studies of any species of the Daesiidae. We performed field and laboratory investigations in order to predict its distribution, to reveal seasonal and circadian activity, habitat preference, burrowing, foraging and post-mating behavior, fecundity, and ontogenetic development. Further, our goal has been to identify morphological characters correlated with sexual dimorphism in order to find measures that could be used to identify the sex of juvenile specimens.

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METHODS

Field collection.—From February to November we monitored pitfall traps (see Cardoso et al. 2004, 2007 for details) in 11 different sites across Portugal over three different years: in 2001 in the northern part (Douro Internacional Nature Park), in 2002 in the central part (Serras de Aire e Candeeiros Nature Park), and in 2003 in the southern part of Portugal (Vale do Guadiana Nature Park). Solifuges occurred in three different habitat types: pseudosteppe or pasture with solitary trees, scrubland, and forest (Table 1). We emptied traps in two-week intervals. Further, we collected solifuges by hand in a garden in Valverde da Mitra (near Évora), southern Portugal. We preserved all captured specimens in 70% ethanol and deposited them in the collection of arachnids at the Department of Botany and Zoology, Masaryk University, Brno.

Altogether, we collected 702 individuals of *G. dorsalis* in the field over the research period, with most of them (78%) coming from southern Portugal, followed by 8% from central, and 14% from northern Portugal. We classified each collected individual to a developmental stage (juvenile or adult) and sex (only adults). Additionally, for each individual, we measured the following four morphological characters: length and the width of propeltidium, number of malleoli (on the ventral side

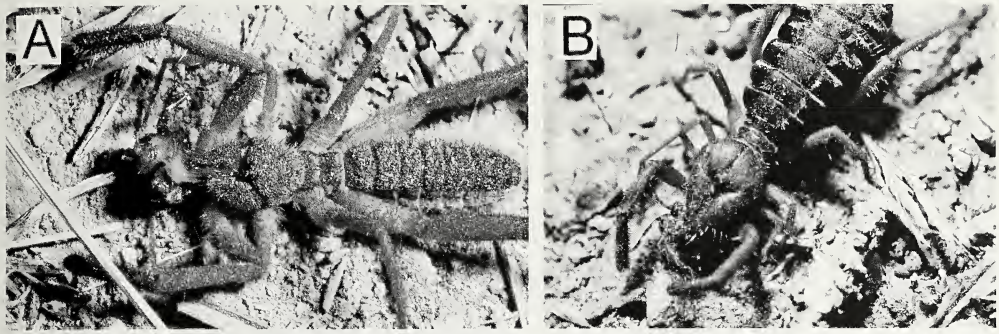

Figure 1.—Adult male (A) and adult female (B) of *Gluvia dorsalis* consuming their prey.

of coxa, trochanter, and femur of the fourth leg), and width of the fourth malleolus at the distal end. These characters were used to distinguish probable instars, to estimate developmental trajectory, and to find sexually dimorphic characters. We chose these characters because they were found to change during development, and their size is constant within intermolt intervals (Junqua 1966).

Potential distribution.—There are a large number of techniques proposed for modeling the predicted potential distribution of species based on presence data for a restricted number of points in space and environmental data for an entire region. In general, they are based on the principle that species are restricted by the environmental conditions they can survive. If we know a number of sites where a species is present, it is possible to create a "suitable climatic envelope" for the species. This climatic envelope is then translated to space through geographic information systems, making it possible to obtain spatial suitable maps for the species. It should be noted, however, that such maps usually only reflect the potential distribution of species, not their true distribution, which may be smaller. This is due to historical (e.g., local extinction, inability to disperse to many regions) or biological (e.g., competition from ecologically similar species) factors. Such factors may limit the effective distribution of species in areas that should be environmentally adequate for their populations. We used the Maxent method (Phillips et al. 2006; Phillips & Dudik 2008) because it uses presence-only data, and because it is considered the most accurate method available (Hernandez et al. 2006). The map of distribution is based on González-Moliné et al. (2008) and unpublished data from the authors (total of 254 records). One-fifth of the records were randomly chosen for a test dataset, not used in the training of the algorithm. The spatial variables used in the modeling were eight bioclimatic variables available from the Worldclim database (Hijmans et al. 2005): annual precipitation, precipitation of the driest and wettest months, precipitation seasonality (coefficient of variation of monthly values), average annual temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, and temperature seasonality (standard deviation of monthly values). Additionally, we used a digital elevation model. All variables had a resolution of one square kilometer.

Field observations.—We investigated circadian activity in June 2005 in Valverde da Mitra, Portugal, for 9 days by censusing active solifuges for 20 min/h from 05:00 to 03:00 h in four 100 m^2 areas. We observed burrowing and prey hunting behaviors in July and September 2006 at the same site.

We obtained data on potential prey by censusing representatives of invertebrate orders occurring on the ground during the major activity period (20.00–24.00 h) on 3 days in June in two 100 m^2 areas. Additionally, we observed natural prey by witnessing prey capture, inspecting the prey, and identifying its remnants to order. Only 15 individuals of 196 inspected were found to have prey in their chelicerae.

Laboratory observations.—To determine diet breadth, we brought 62 individuals (20 males, 20 females, 22 juveniles) into the laboratory and put them in individual dishes (8 cm diameter, 4 cm tall) with a thin layer of sand substrate and a lightly moistened piece of gauze. We offered solifuges various arthropods (Table 2) found in the study site. The prey was

Table 1.—Overview of 11 study sites in three nature parks in Portugal according to their habitat classification.

	Nature park		
Habitat type	Douro Internacional	Serras de Aire e Candeeiros	Vale do Guadiana
Pseudosteppe or pasture	Vila Chã da Braciosa	–	Algodôr Braciais
Scrubland	Picote	Vale Garcia	Corredoura Ribeira de Limas
Forest	Fonte d'Aldeia	–	Cerro das Antenas, São Domingos, Perímetro Florestal de Mértola

Table 2.—Attack and feeding frequencies on a variety of prey offered to large juvenile and adult specimens of *G. dorsalis* in the laboratory. *n* = sample size, Size = length of prey.

Order	Family, Genus, Species	*n*	Size [mm]	Attack [%]	Feeding [%]
Acari	*Trombidium* sp.	10	2.5–3.5	20	0
Solifuges	*G. dorsalis*	38	15–22	100	100
Araneae	Agelenidae, Araneidae, Corinnidae, Filistatidae, Gnaphosidae, Lycosidae, Theridiidae	62	15–22	83.9	83.9
Opiliones	*Leiobunum* sp.	5	2	100	100
Isopoda	*Armadillidium* sp.	10	7–11	20	0
	Porcelio sp.	10	10	70	70
Diplopoda	Julidae	14	16–21	16.7	0
Thysanura	*Lepisma* sp.	9	7.5–9	77.8	77.8
Ephemeroptera	unidentified	11	7.5–11	27.3	27.3
Dermaptera	*Forficula* sp.	2	9	100	100
Ensifera	*Acheta domestica*	52	6–25	100	100
Caelifera	unidentified	45	5	93.3	93.3
Isoptera	*Reticulitermes* sp.	10	3.5–4	80	80
Heteroptera	*Coreus* sp., *Lygus* sp.	35	4–12	88.6	80
Coleoptera	*Tenebrio molitor* larvae	41	5	100	100
	Brachinus crepitans adults	12	9	0	0
	other Carabidae	42	4.5–16	47.6	45.2
Diptera	Muscidae	10	5.5–9	90	90
Hymenoptera	*Tapinoma* sp.	8	2–3	100	100
	Camponotus sp.	10	9–13	20	0
	Messor sp.	17	6–9	64.7	64.7
Lepidoptera	Noctuidae adults	10	8.5–15	60	50

offered to each solifuge in a random order in one-day intervals. For each feeding trial we recorded the size of prey, whether it was attacked and consumed, and noted the predatory behavior. We replaced a prey item that was not attacked within 5 min with another one. Once the prey was consumed, we cleaned the prey remnants from the dishes.

Adult males (n = 39) and adult females (n = 21) were captured in the field in June and then mated in the laboratory (see Hrušková-Martišová et al. 2010). We paired each female successively with one to four males until it mated. After successful copulation, we placed female solifuges singly in vials (5 cm diameter, 8 cm tall) with a sand layer (2 cm deep) with darkened sides, to lay eggs. The vials were kept in a chamber at 23° C (humidity was not measured) until hatching. The sand substrate was moistened once a week by few drops of water. We checked egg clutches every day during the three following months. We counted and measured (diameter) 10 eggs in each clutch. Larvae were kept in conditions similar to the eggs until molting to the first instar, for which we measured morphological characters similarly to the adults (see above).

Data analysis.—We studied the effect of average monthly precipitation and average monthly temperature on seasonal activity using multiple regression within Generalized Linear Models with Poisson errors (GLM). Data on long-term average monthly temperatures and average monthly precipitation were those for Évora, because most of the material came from Alentejo and this was the nearest place for which meteorological data were available at www.worldclimate.com. We compared the relative composition of potential and actual prey using chi-square tests. We used the Spearman correlation to study the relationship between the size of eggs and the clutch size. For the analyses of sexually dimorphic characters, we used specimens from all study sites, because there was no significant difference in the propeltidium width of adult males or females between locations (ANOVA, $F < 0.8$, $P > 0.46$). Models of the relationship between selected morphological characters for juveniles, males, and females were compared by means of ANCOVA. We performed all analyses in R (R Development Core Team 2009). We present means and their standard errors in the text. We estimated confidence intervals (CI_{95}) using normal approximation.

RESULTS

Distribution and habitat preference.—*Gluvia dorsalis* specimens have been collected throughout most of the Iberian Peninsula (Fig. 2). This is reflected in its predicted presence in all but the northern and northwestern regions and the highest mountain chains. As previously mentioned, the output of Maxent, or any other technique, are maps of predicted distribution based on current climate suitability and not realized distributions, which can be smaller due to historical or biological reasons. The AUC (area under curve) of the ROC (Receiver Operating Characteristic) plot of the test dataset was 0.815 in a scale of 0 to 1, where 0.5 represents a random prediction, indicating that the maps can be considered as relatively accurate. The variable found to be most strongly driving the species distribution was the precipitation of the driest month.

According to our abundance data collected in Portugal, the species shows a strong preference for open-grass plains with low vegetation, such as pseudosteppes or pastures (55%, n = 643) or slopes with low-height shrub cover (39%). Only 6% of the individuals were found in forested (*Quercus* or *Eucalytus*) areas.

Seasonal and circadian activity.—Solifuges were found to be active from late May until the beginning of November (Fig. 3). Their activity was negatively correlated with monthly average precipitation (GLM, X^2 = 227, df = 1, $P < 0.0001$,

Figure 2.—Potential distribution of *G. dorsalis* on the Iberian Peninsula. Darker shades represent higher suitability for the species. Points represent actual records.

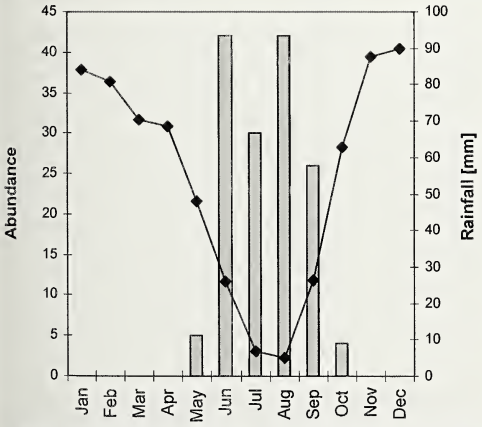

Figure 3.—Seasonal activity (i.e., total abundance per month [bars]) of *G. dorsalis* and the mean monthly precipitation (points).

Fig. 3) and positively correlated with monthly average temperature (GLM, $X^2 = 8.5$, $df = 1$, $P = 0.004$). The adult males and females appeared in late May and were most abundant in June and July. Males disappeared in mid-August, and females disappeared a month later. The average sex ratio (males: females) was highly skewed in favor of females (0.38, $n = 157$) in the field (Binomial test, $P = 0.004$).

G. dorsalis are strictly nocturnal (Fig. 4). Individuals emerge after sunset and are active until midnight, with an activity peak between 21:00 and 22:00 ($n = 68$). Principal activities observed included prey-capturing or burrow-digging. During the rest of the day solifuges hid in stonewall crevices, in shallow depressions under stones, or in the debris. Two individuals that we observed running on the ground during the day were presumably disturbed when we stepped on the rocks where they had hidden.

Burrowing behavior.—We observed females ($n = 20$) and juveniles ($n = 9$), but no males, digging burrows between 22:00 and 24:00 h in sandy soil. Solifuges dug and raked the loose sand, mainly with the second pair of legs. Chelicerae, pedipalps, and the first pair of legs were shaped into a basket to push sand heaps aside to a distance of a few centimeters.

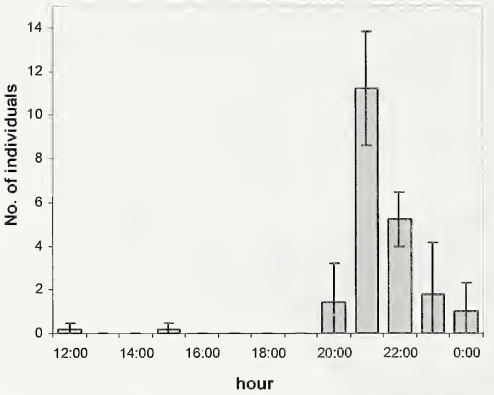

Figure 4.—Mean number (±SE) of individuals per hour found during 20 min in Mitra. Time of inactivity (01:00–11:00 h) are not shown.

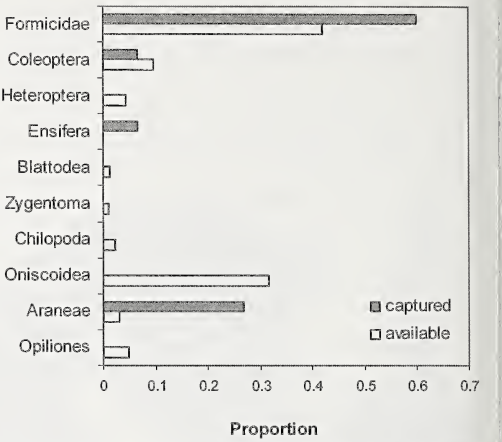

Figure 5.—Comparison of available and captured prey. Bars represent proportion of individuals. There were 3,254 prey individuals available and 15 prey captured.

They repeated these movements until completing the burrow. All burrows had open entrances.

Prey and prey capture.—Hunting solifuges, juvenile or adult, ran quickly over the ground with thte pedipalps and first pair of legs stretched forward. The movement appeared haphazard, with frequent changes in direction. Once prey was encountered, solifuges seized it quickly by means of the sucking organs on the pedipalpal tips, and subsequently grasped it with the chelicerae. Solifuges grasped bodies of small prey, but legs of large prey (e.g., grasshoppers). The prey sometimes escaped by pulling away from its own leg. In all cases we observed, the solifuges remained at the site of capture while eating the prey.

In the field, we found the main available (potential) prey on the ground to be ants (42%, $n = 325$), woodlice (32%), and beetles (10%), but we observed solifuges catching mainly ants and spiders in such conditions. The captured prey, therefore, differed from the available options ($X^2 = 47.4$, $df = 9$, $P < 0.0001$, Fig. 5).

In the laboratory, solifuges accepted and consumed a wide variety of arthropods ranging in size from 2 to 25 mm (Table 2), so that the relative size (prey to solifuge) was between 0.2 and 1. Solifuges rejected or attacked but did not consume mites, some woodlice, millipedes, large ants, and carabid beetles. Male solifuges further rejected hard sclerotized beetles. In the laboratory, solifuges accepted a wider prey variety than was available in the field.

Oviposition and ontogenetic development.—In June, on average 11 days (SE = 0.7, $n = 11$) after mating, females produced one clutch of spherical, whitish eggs. They deposited a mass of eggs on the surface of the sand in the vials. The clutch size varied from 47 to 163 eggs (mean = 83.4, $n = 11$), and the eggs had an average diameter of 1.78 mm (SE = 0.09, $n = 96$). The size of the eggs was not related to the clutch size (Spearman correlation, $\rho = -0.3$, $S = 26$, $P = 0.68$). The females died on average 9 days (SE = 2.5, $n = 11$) following the oviposition. In one case, the female was observed laying another clutch (10 eggs) one week after the first one (137 eggs) had been deposited.

On average, 56 days (SE = 4, $n = 85$) after laying eggs, pale yellow immobile larvae hatched. These inactive individuals molted into the first non-feeding instar, on average in 17 days (SE = 0.9, $n = 25$). Measurements of the morphological characters of the first instar are shown in Table 3. Juveniles captured in the field were separated into two ontogenetic categories based on the number of malleoli: as early juveniles with 3 malleoli, and later juveniles with 5 malleoli. In the field, the smallest early instars (propeltidium width <1 mm) occurred from mid-July to mid-October (Fig. 6). The occurrence of early and late juveniles overlapped, as they occurred every month from May to October.

Because we sampled early juveniles, late juveniles, and adult stages each month from June to August, we assume that the life cycle is biennial, with a longevity of about 700 days. We suggest two extreme developmental trajectories. Specimens that hatched into the first instar in mid-July (dashed line in Fig. 6) would probably pass through 2–3 instars before overwintering to reach about 1.8 mm (propeltidium width). Next season, these specimens would pass through several instars to reach about 3.7 mm (propeltidium width) before the onset of winter, so that the following season they would reach maturity in the beginning of June. Specimens that hatched into the first instar later, in late September, did not molt and overwintered at 1.2 mm (propeltidium width). Next season they would pass through a few instars to reach 3 mm (propeltidium width). In the following season they would pass through another few instars to reach adulthood in August.

Sexual dimorphism.—Adult males ($n = 55$) were smaller and had a narrower propeltidium and wider malleoli than adult females ($n = 66$) (Table 3). Male sclerotized body parts (prosomatic parts and appendages) were densely covered with

Table 3.—Measurements (mean ± SE) of some body traits in the first-instar specimens, adult males and adult females of *G. dorsalis*.

Character	First instars (n = 10)	Males (n = 55)	Females (n = 66)
Length of propeltidium [mm]	0.797 ± 0.047	2.024 ± 0.363	2.728 ± 0.441
Width of propeltidium [mm]	1.061 ± 0.087	2.778 ± 0.405	4.495 ± 0.701
Number of malleoli	3	5	5
Width of the fourth malleolus [mm]	0.230 ± 0.040	0.945 ± 0.129	0.835 ± 0.128
Malleolus to propeltidium width ratio	0.216 ± 0.030	0.355 ± 0.038	0.188 ± 0.026

spines, while those of females were not (Fig. 1). The relationship between the width of propeltidium and width of malleoli was isometric for females, but allometric for males (Fig. 7A). The malleoli size of females increased with propeltidium size in similar fashion to juveniles (ANCOVA, $F_{2,650}$ = 0.91, P = 0.4). But in males the relationship was significantly steeper than in juveniles (ANCOVA, $F_{2,652}$ = 1021, $P < 0.0001$, Fig. 7A), suggesting that the size of malleoli increased markedly at the last molt of males. The relationship between the width and length of propeltidium was, in turn, isometric for males, but allometric for females (Fig. 7B). For juveniles, this relationship was significantly different from that of females (ANCOVA, $F_{2,527}$ = 13.3, $P < 0.0001$) as well as males (ANCOVA, $F_{2,527}$ = 72.5, $P < 0.0001$, Fig. 7B). Clearly, there was a change in the shape of propeltidium at the last molt in both sexes. The ratio of width to length of propeltidium was 1.62 (CI_{95} = 1.59, 1.65) in females and 1.37 (CI_{95} = 1.32, 1.41) in males.

DISCUSSION

We found that *Gluvia dorsalis* is widespread on the Iberian peninsula, but has a quite restricted seasonal activity. It feeds on a variety of epigean arthropods that are captured only during the first three hours of the scotophase. Its reproduction occurs at the beginning of summer, and the life cycle is probably biennial. Several morphological characters revealed apparent sexual dimorphism at maturity, such as shape of the propeltidium or size of malleoli. We will now compare traits studied with those from other solifuge families, as there are few comparative data.

Our results strongly suggest that the distribution of the solifuge *G. dorsalis* is mostly limited to areas of the Iberian Peninsula with scarce summer rain. This supports the fact that solifuges are restricted to arid environments of the world at variable altitudes and temperatures. Similar to other solifuge species (Griffin 1990; Punzo 1998b), *G. dorsalis* has a marked preference for habitats of a semi-desert character (González-

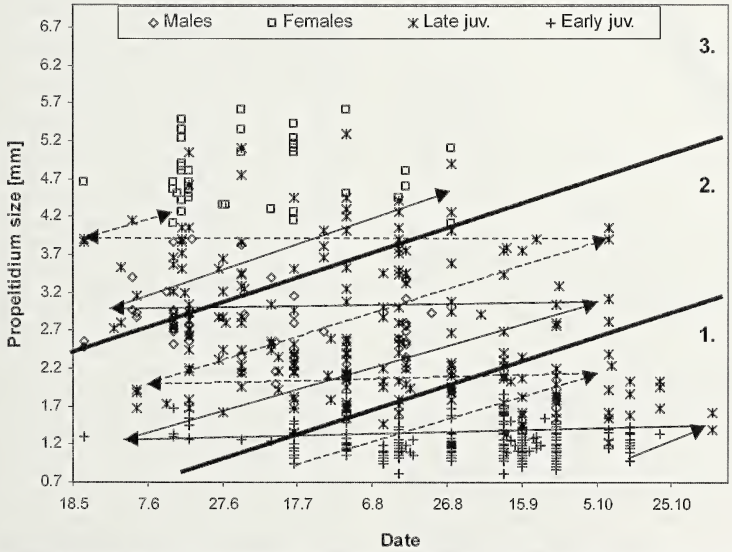

Figure 6.—Relationship between the size of propeltidium (width) and the occurrence of adult males, adult females, late juveniles (with 5 malleoli), and early juveniles (with 3 malleoli) during season from May until October. Bold lines mark the hypothesized borders between three consecutive seasons (1., 2., 3.). The slopes of the bold lines are parallel with two extreme hypothesized developmental trajectories displayed by thin solid (for late hatchlings) and thin dashed (for early hatchlings) lines with arrows.

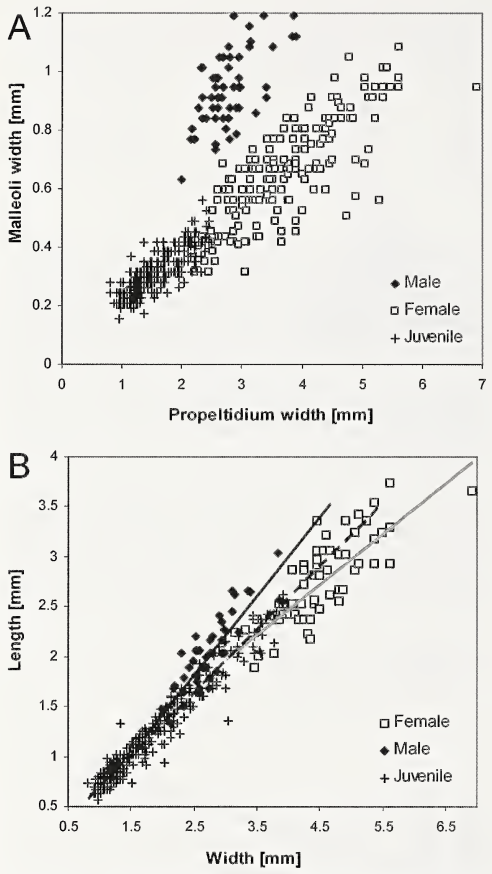

Figure 7.—A. Relationship between the width of malleoli and the width of propeltidium for juveniles, adult males and females. B. Relationship between the length and width of propeltidium for juveniles, adult males and females with linear models. Males = solid line, females = gray line, juveniles = dashed line.

Moliné et al. 2008; this study): sand substrate, rocks, and low and sparse vegetation cover. Females and juveniles can easily dig burrows in the sand, whereas stones, grass and shrubs provide cover and protection for the males. Although the use of burrows as retreats during the periods of inactivity and oviposition is widespread among solifuges (Muma 1966b; Cloudsley-Thompson 1977; Punzo 1998b; Hrušková-Martišová et al. 2007), our field observations show that solifuges sheltered mainly under stones, in debris and rock crevices while resting during the day and as a protection during ecdysis. Burrows were excavated exclusively by juveniles and females; thus, we expect that burrows function for overwintering and for egg deposition. Similar observations were made by Punzo (1998c) of *Eremobates marathoni* Muma 1951 (Eremobatidae), where females were found in the non-plugged burrows, while males utilized simple depressions under a rock or decaying vegetation. The burrowing behavior of *G. dorsalis* was generally similar to that reported for other solifuge species (Hingston 1925; Junqua 1966; Muma 1966b; Cloudsley-Thompson 1977; Gore & Cushing 1980).

Their preference for dry habitats is also reflected in their restricted seasonal activity. As revealed by previous studies (Rambla & Barrientos 1986; González-Moliné et al. 2008), *G. dorsalis* was active during months with the highest temperature and very few summer rains, like many other solifuge species (Heymons 1902; Cloudsley-Thompson 1961a; Wharton 1987; Chandra 1989; Punzo 1997). Although both these variables are strongly correlated, rainfall was found to be a better predictor of their seasonal activity pattern than temperature. It is not clear why rain can limit the seasonal occurrence of solifuges. We have observed that on rainy nights in late summer, the density of their prey, such as ants, decreased dramatically. So solifuges may avoid wet days due to low profitability resulting from a low capture rate.

High abundance of prey must be very important for *G. dorsalis*, because its foraging activity period is very short, lasting only about three hours. Whether such a short period is an adaptation to avoid desiccation or predators is not clear. Berland (1932) and Lawrence (1956), however, suggested that *G. dorsalis* is a day-active species, because it is small. Nocturnal activity is very common in many other solifuge species (e.g., Turner 1916; Lawrence 1955; Cloudsley-Thompson 1961a; Hrušková-Martišová et al. 2007; Punzo 1998b), as well as many other animals inhabiting arid environments (Cloudsley-Thompson 1991; Rose & Mueller 2006).

The majority of solifuge species has been reported to be extremely active and extraordinarily voracious predators (Muma 1966c); however, researchers have made only a few observations on solifuge foraging behavior and feeding habits under natural conditions (Turner 1916; Bolwig 1952; Wharton 1987; Hrušková-Martišová et al. 2007). In most of those studies, juveniles and/or adults were observed to search and hunt their prey on the ground. Our observations indicate that hunting, capturing, and handling prey in *G. dorsalis* are similar to descriptions for other solifuge species (Hutton 1843; Turner 1916; Bolwig 1952; Cloudsley-Thompson 1961b; Punzo 1995). *G. dorsalis* is clearly a polyphagous predator, as are other solifuge species (Turner 1916; Muma 1967; Cloudsley-Thompson 1977; Wharton 1987; Punzo 1994, 1997). In the field, the diversity of captured prey was lower than in the laboratory, reflecting the restricted availability. *Gluvia dorsalis* seems to prefer soft-bodied prey smaller than itself, refusing arthropods with chemical or other types of defenses like in other solifuge species (Punzo 1993, 1994). It is probable that there is frequent cannibalism of small specimens by larger ones.

The longevity of solifuges is largely unknown. Some authors have suggested that they are univoltine and do not live for more than one year (Muma 1963, 1966a; Punzo 1998a). But Wharton (1987), using data from pitfall traps and field observations, concluded that *Metasolpuga picta* (Kraepelin 1899) is biennial. Junqua (1966) observed in the laboratory that *Othoes* molted once a month. Having 8–10 instars, this

species lived for ~3 yr. Lawrence (1963), studying change in the cheliceral teeth, concluded that *Zeria monteiroi* (Pocock 1895) live for several years. Our data suggest that the longevity of *G. dorsalis* is about 2 yr. Although it is as large as *E. marathoni* (Punzo 1998a), *G. dorsalis* has longer life cycle, likely due to longer hibernation period.

In the laboratory we observed that the embryological development lasted almost 2 mo. We assume that in natural conditions development is much shorter because the ambient temperature is much higher than it was in laboratory. Based upon our previous experience, we avoided using higher temperature to avoid egg desiccation (if kept in dry conditions) or attack by fungi (if kept in humid conditions), both conditions accelerated by higher temperatures. As mating takes place in mid-June and the first instars were found in pitfall traps in mid-July, it appears that the incubation period together with the larval development takes about one month in nature. In a similarly large *E. durangonus* Roewer 1934, the average duration of intermolt interval was 25 days at 20° C. Assuming a similar duration for *G. dorsalis* and considering the temperature records over the season in Portugal, we expect that individuals that hatched in mid July would molt about 2–3 times before overwintering, then continue to molt next season about 4–5 times, finally molting into the adult stage the next season. There would thus be 7–9 juvenile instars altogether. This corresponds closely to the rate observed for *E. marathoni* (i.e., increase in propeltidium length by 37% on average [Punzo 1998a]).

We were not able to distinguish particular juvenile instars due to the large variation in all measured morphological traits. The only discrete character was the number of malleoli: three in early stages and five in later juvenile stages and in adults. Junqua (1966) and Muma (1966a) observed that the juveniles of the first to the fourth instars exhibit three pairs of malleoli and the fifth to the ninth instars possess five pairs. Our data appear to be in agreement with their conclusions.

In most of the solifuge species studied to date, males and females differ in body size, in the presence of sex-specific structures, and in shape and size of some body structures (Punzo 1998b). In *G. dorsalis*, we found conspicuous sexual dimorphism in total body setosity, propeltidium, and malleoli size. We suspect that some features might already be dimorphic in the juvenile stages. However, the size of malleoli and the shape of propeltidium (expressed as width to length ratio) become clearly dimorphic only in the adult stage. However, certain differences in the shape of propeltidium were already apparent in the juvenile stage. This character deserves further investigation because it might be used for the recognition of sex in juvenile instars.

By revealing basic natural history data of *G. dorsalis*, we raise many questions, such as why their foraging activity is so short, what portion of their diet involves cannibalism, or how long is their life cycle. These remain to be addressed in future studies. Unfortunately, the scarcity of individuals in nature and the difficulty of observing and rearing them makes investigation of these remarkable arachnids infeasible.

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Whip spiders of the genus *Sarax* in the Papuan region, with description of two new species (Amblypygi: Charinidae)

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Abstract. Three species of the genus *Sarax* are recognized in the Papuan region. Among them, two species, *Sarax newbritainensis*, new species, from New Britain, and *S. monodenticulatus*, new species, from Waigeo Island are described. *Sarax newbritainensis* resembles *S. willeyi* in having the same number of denticles on the pedipalpal tarsus, but they distinctly differ from each other in body size, form of carapace, length of legs and number and arrangement of the trichobothria of tibia of leg IV. *Sarax monodenticulatus* is distinguished from the other two Papuan species by possessing a single denticle on the pedipalpal tarsus. The taxonomic status and the natural history of the species are discussed.

Keywords: Taxonomy, Waigeo Island, Batanta Island, New Britain, Papua New Guinea, Indonesia

Whip spiders, or Amblypygi, are flattened arachnids characterized by their raptorial pedipalps and the first legs modified into extremely elongate antenniform appendages (Weygoldt 2000). They are mostly active during the night and hide under stones and fallen trees during the day. A total of 143 species belonging to 17 genera in five families are currently known (Harvey 2002, 2003; Armas & Gadar 2004; Weygoldt 2002; 2006; Rahmadi & Harvey 2008). Of these, ten species and two subspecies belong to the charinid genus *Sarax* Simon 1892, which is known from the Oriental and Papuan region (India to the Solomons) (Harvey 2003; see also Weygoldt 2005:12).

Kraepelin (1895) recorded *Sarax sarawakensis* (Thorell 1888) from New Guinea and Solomon Islands, and Pocock (1898) recorded the species from New Britain based on specimens procured by Dr. A. Willey, the director of the Colombo Museum at that time. Gravely (1915) described *S. willeyi* based on the two specimens "preserved in the Indian Museum" and "collected by Dr. Willey in New Britain."

The other charinid genus occurring in the Papuan region is *Charinus* Simon 1892. The genus occurs pantropically with 35 species and in the Papuan region only one species, *Charinus papuanus* Weygoldt 2006, is known, from the type locality near Port Moresby, Papua New Guinea (Weygoldt 2006).

During a study on whip spiders collected during the "Ekspedisi Widya Nusantara (e-WIN Expedition)" to Raja Ampat Island, West Papua (organized by the Indonesian Institute of Sciences in 2007 and 2008), and based on the examination of some additional specimens from Papua New Guinea and New Britain and the holotype of *Charon sarawakensis* (= *S. sarawakensis*), we recognized three distinct species of *Sarax* in the Papuan region. Two of them are described here as new to science, and the taxonomic status of *S. willeyi* is discussed.

METHODS

Specimens from the e-WIN expedition examined in this study were preserved in 90–95% ethanol and others in 70–80%. General terminology and pedipalpal spination follow Weygoldt (2000), and pedipalpal terminology follows Harvey and West (1998). We made the measurements (in mm) and drawings using, respectively, an ocular micrometer and a drawing tube mounted on a stereoscopic dissecting microscope (Olympus SZX12). To prepare the digital images of the carapace, we compiled multiple focal planes taken with a digital microscope (KEYENCE VH-5500) using the software Helicon Focus 4.70 (Helicon Soft Ltd. 2009: online at http://www.heliconsoft.com/heliconfocus.html). In order to examine the structure of genitalia we lifted the genital operculum. The acronyms of the museums/institutions are as follows: MCSG, Museo Civico di Storia "Giacomo Doria," Genova, Italy; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, USA; MZB, Museum Zoologicum Bogoriense, Cibinong, Indonesia; MNHN, Museum National d'Histoire Naturelle, Paris, France.

The holotype female of *Sarax sarawakensis* (Thorell 1888), lodged in MCSG and labeled "*Sarax saravakensis* Thor. Sarawak, Viag Doria and Beccari" was examined to compare with the three *Sarax* species treated below.

KEY TO THE CHARINID WHIP SPIDERS OF THE PAPUAN REGION

1. Abdominal sternite III without ventral sac covers ..... *Charinus papuanus* Weygoldt
   Abdominal sternite III with ventral sac covers ..... *Sarax*...2
2. Body reddish-brown. Tibia of leg IV with 17 trichobothria (Fig. 4d); pedipalpal tarsus with one denticle (Fig. 4b) ..... *Sarax monodenticulatus* new species
   Body pale brown or dark greenish-brown. Tibia of leg IV with 17 or 19 trichobothria; pedipalpal tarsus with two denticles (Figs. 2c, 3b) 3

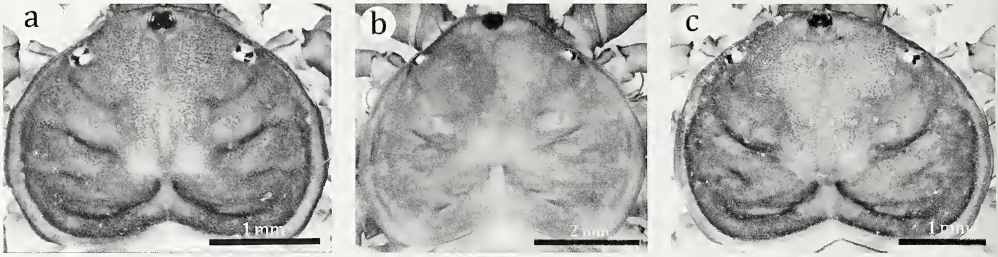

Figure 1.—Carapace. a, *Sarax willeyi* from Batanta Island; b, *Sarax newbritainensis*, holotype from New Britain; c, *Sarax monodenticulatus*, holotype from Waigeo Island.

3. Body pale brown. Legs elongate; tibia of leg IV with 19 trichobothria (Fig. 3e); trichobothrium *bt* close to distal margin; metatarsus of leg I 1.5 times as long as the first tarsal segment . . . . . *Sarax newbritainensis* new species
Body dark greenish-brown. Legs not elongate; tibia of leg IV with 17 trichobothria (Fig. 2d); trichobothrium *bt* locating at about mid-length of fourth basitibial segment; metatarsus of leg I as long as the first tarsal segment . . . . . *Sarax willeyi* Gravely

TAXONOMY

Family Charinidae Quintero 1986
Genus *Sarax* Simon 1892

Sarax Simon 1892:43, 48; Kraepelin 1895:45; Kraepelin 1899:250; Pocock 1900:131; Gravely 1915:441; Mello-Leitão 1931:55; Werner 1935:471; Weygoldt 2000:25; Harvey 2003:7.

Phrynichosarax Gravely 1915:437; Mello-Leitão 1931:52 (as *Phrynicosarax* [sic]); Werner 1935:470; Weygoldt 2000:25 (synonymized with *Sarax*); Weygoldt 2002:146.

Type species.—*Sarax: Sarax brachydactylus* Simon 1892, by original designation.

Phrynichosarax: Phrynichosarax cochinensis Gravely 1915, by original designation.

Diagnosis.—Small to medium-sized whip spiders; adult body length 4–10 mm. Pedipalpal patella with three large primary spines, the distal spine largest, subsequent spines becoming shorter proximally; ventral sac covers present on abdominal sternite III. Lateral eyes close to lateral margin of carapace. Basitibia of leg IV consisting of three or four segments.

Remarks.—The family Charinidae currently consists of the following three genera: *Sarax*, *Catageus* Thorell 1889 with a single species from Myanmar, and *Charinus* consisting of 35 species with a circum-tropical distribution (Harvey 2003; Weygoldt & Van Damme 2004; Weygoldt 2006). *Sarax* is, in general, similar to *Charinus*, especially in the pedipalpal patella spination, but clearly distinguished by the presence/absence of the ventral sac cover; in *Sarax* the ventral sac cover is present, while it is absent in *Charinus*. *Catageus* can be distinguished from the other two genera by the second spine of the pedipalpal patella being the largest (in other two genera, the first is the largest) and the proximal spine of the antero-dorsal pedipalpal tibia being larger than the distal one (Weygoldt 2000).

Sarax willeyi Gravely 1915
(Figs. 1a, 2a–g)

Sarax willeyi Gravely 1915:441, fig. 7; Mello-Leitão 1931:55; Werner 1935:471; Kraus 1970, figs. 10–11; Harvey 2003:9.

Material examined.—INDONESIA: *West Papua Province*: 3 females (MZB.Ambl.119–120 and 121 [ovigerous]), under stone in forest near Gua Eleg (00°53.51′S, 130°40.06′E, 156 m asl.), Wailebet, Raja Ampat Regency, Batanta Island, 1 May 2008, C. Rahmadi; 4 males (MZB.Ambl.122, 125–127), 1 female (MZB.Ambl.123, ovigerous with 7 eggs), under stone in small limestone forest near Gua Umso (00°49.89′S, 130°53.82′E), Yenanas, Raja Ampat Regency, 27 April 2008, C. Rahmadi; 1 male (MZB.AMbl.128), Solol Village, Salawati Island, 7 May 2008, C. Rahmadi. PAPUA NEW GUINEA: *Madang Province*: 2 males, 3 females (MZB.AMbl. 129–133), 2 males, 2 females (MCZ DNA104752), Madang Bitabag Reserve, (05°08′19.3″S, 145°46′28.2″E, 109 m asl.), 28 March 2006, R.M. Clouse, Ulai & Nataniel.

Diagnosis.—*Sarax willeyi* differs from other congeneric species from the region by its small size (adult body length about 4.0–6.2 mm) and dark greenish-brown body. The legs are proportionally shorter than other species. The pedipalpal tibia has two spines on the antero-dorsal margin; the proximal spine more than half as long as the distal one. Pedipalpal tarsi with two denticles; proximal denticle about half as long as distal one. Tibia of leg IV with 17 trichobothria; trichobothrium *bc* much closer to *bf* than to *sbf*, and *bt* at about mid-length of the fourth basitibial segment (Fig. 2d). The metatarsal segment of leg I as long as the subsequent two segments together.

Description.—*Male:* Color in alcohol. Carapace dark greenish-brown with yellow marks centrally. Pedipalps and legs green except as follows: major spines of pedipalps light brown; tibia and tarsus of leg I with yellow annulations; distal and proximal margins of basitibiae of Legs II–IV brown; distibiae and tarsi of Legs II–IV light green. Abdomen green with brown spots on each tergite.

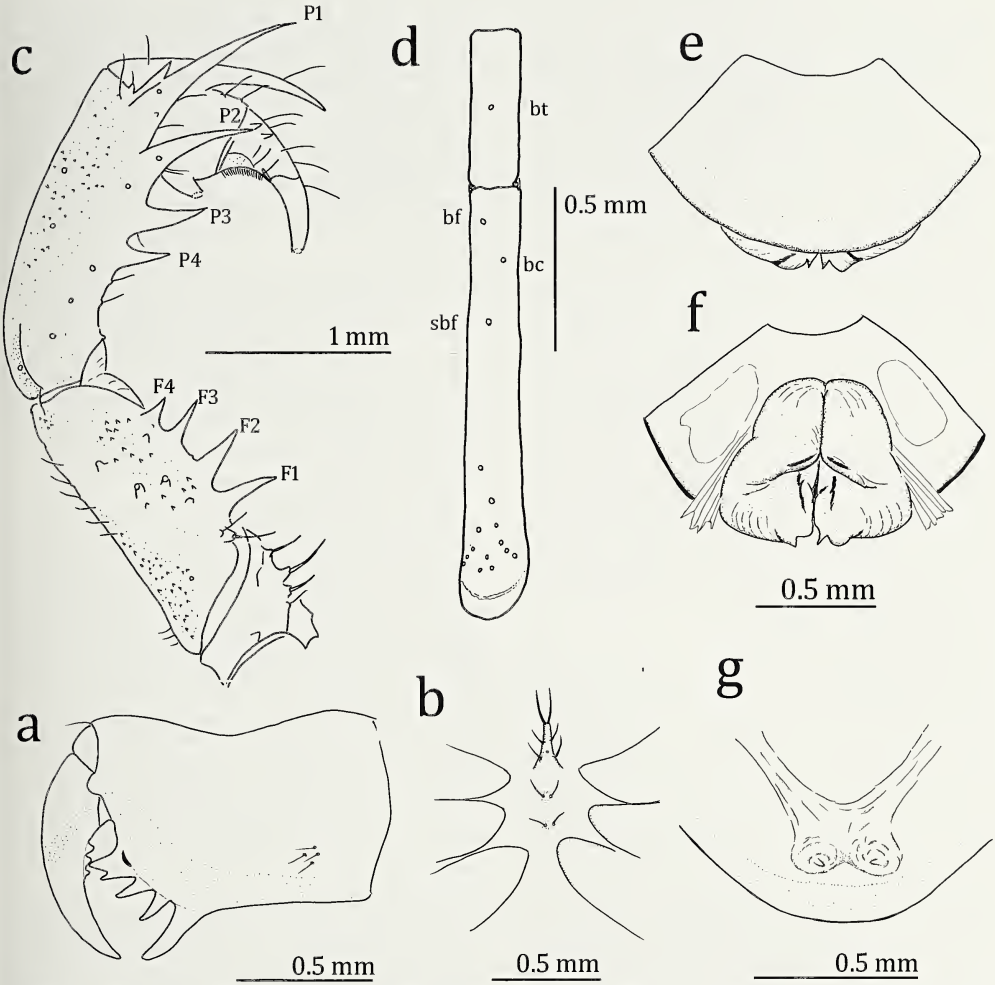

Figure 2.—*Sarax willeyi*, from Batanta Island. a. External view of left chelicera; b. Sternal area of carapace, ventral view; c. Antero-dorsal view of left pedipalp; d. Arrangement of trichobothria on the fourth basitibial segment and distibia of leg IV; e, f. Male genitalia (e. ventral view; f. dorsal view); g. Dorsal view of female gonopods.

Carapace (Fig. 1a): Width about 1.5 times length; surface finely granulate, without setiferous tubercles; median sulcus deep in posterior one-fourth of the carapace, three sulci running laterally on each lateral half of carapace; flange wide and bend upward; anterior margin rounded, with six fine frontal setae. Median eye tubercle black, without apical setae, slightly emarginated antero-medially to form heart shape; median eyes facing antero-laterally. Lateral eye close to lateral margin of carapace.

Chelicera (Fig. 2a): Dorsum smooth, with one fine frontal seta and three fine lateral setae. Basal segment with four teeth: lowermost tooth largest, uppermost tooth bicuspid, with upper cusp larger than lower cusp; inner surface with seven setae arranged in vertical row; outer surface with small blunt tooth opposite bicuspid tooth and four setae near proximal margin. Movable hand with three teeth about equal in size.

Sternum (Fig. 2b): First sternite (= tritosternum) elongate, with paired apical, median and strong basal setae; second

and third sternites rounded and flattened, with paired apical setae.

Pedipalp (Fig. 2c): Short and stout. Trochanter with four setiferous tubercles arranged in a row along antero-dorsal margin, one spine medially and four setiferous tubercles on antero-ventral margin; ventro-anterior apophysis equipped with ten setiferous tubercles present on distal margin of trochanter. Femur with four major spines, some setiferous tubercles and small tubercles in the antero-dorsal part, length of spine F1>F2>F3>F4; area without setiferous tubercles or small tubercles forming narrow band running lengthwise from proximal to distal margin; four major spines, several minor spines and small tubercles on antero-ventral margin; one spine present dorsally of FI and as long as 3/4 length of FI, length of spine FI>FII>FIII, three minor spines between FI and FII. Patella with four major spines, several minor spines, several setiferous tubercles and small tubercles on antero-dorsal margin; length of spine P1>P2>P3>P4, two minor spines (one in several specimens) between P1 and distal margin of patella; three major spines, several setiferous tubercles and small tubercles on antero-ventral margin, length of spines PI>PII>PIII. Tibia with two major spines on antero-dorsal margin, length of proximal spine more than half that of distal one; one major spine on antero-ventral margin close to distal margin of tibia; outer surface of the tibia with several setiferous tubercles, finely granulate. Tarsus completely divided (claw clearly demarcated by articulation), with two denticles on antero-dorsal margin; proximal denticle about 3/4 as long as distal denticle; cleaning organ ventrally with about 30 modified hairs; apotele present.

Legs (Fig. 2d): Femora of Legs I–IV with small tubercles bearing setae. Tibia and tarsus of leg I consisting of 23 and 41 segments, respectively; tibiae of Legs II and III two-segmented; basitibia of leg IV four-segmented, fourth segment with one trichobothrium (value in parentheses: ratio of the distance from the trichobothrium to the proximal margin of the segment against the length of the segment), *bt* (0.50); distitibiae of Legs II–IV each with 16 trichobothria (Fig. 2d), *bf* (0.07), *sbf* (0.31), *bc* (0.17), *bt* at about mid-length of the segment, *bc* close to *bf* than to *sbf*. Tarsi of Legs II–IV four-segmented; first segment about as long as length of subsequent three segments combined; second segment with light-yellow transverse line; fourth segment without oblique slit; pulvilli present.

Genitalia (Figs. 2e, f): Covered ventrally by genital operculum; paired apically-pointed small median projections present at posterior margin; two brown marks present near the base of projections (Fig. 2e). In dorsal view, paired anteriorly-rounded brown bands present; paired weakly-sclerotized brown markings present medially (Fig. 2f).

Female: Similar to the male. Gonopods with paired finger-like apically pointed projections (Fig. 2g).

Measurements.—Male (n = 7), [female (n = 9)]; values for segments of the appendages are their lengths. Body length (excluding chelicera) 4.00–6.20 [4.04–6.95]. Carapace: median length 1.75–2.40 [1.48–2.70]; width 1.50–3.60 [2.08–3.75]; median eyes to anterior margin of carapace 0.04–0.05 [0.04–0.05]; distance between lateral eyes 0.92–1.72 [0.80–1.75]; lateral eye to anterior margin of carapace 0.25–0.40 [0.20–0.40]; lateral eye to lateral margin of carapace 0.08–0.25 [0.04–0.25]. Pedipalps: trochanter 0.40–0.80 [0.32–0.75]; femur 1.00–2.28 [0.70–1.90]; patella 1.00–2.60 [1.00–2.40]; tibia 0.40–1.25 [0.28–1.00]; tarsus 0.40–1.00 [0.60–1.25]. Leg I: femur 2.50–4.60 [4.60]; patella 0.35–0.50 [0.32–0.50]. Leg II: femur 1.75–3.20 [1.48–3.25], patella 0.48–0.70 [0.40–0.75]; basitibia 2.08 [0.80–2.25]; distitibia 1.60 [0.84–1.50]; metatarsus + tarsus 1.60 [0.88–1.50]. Leg III: femur 2.25–3.60 [1.68–3.75]; patella 0.48–0.70 [0.40–0.75]; basitibia 1.15–2.80 [1.20–3.00]; distitibia 1.28–1.80 [1.00–2.00]; metatarsus+ tarsus 1.05–1.60 [1.00–2.00]. Leg IV: femur 1.85–3.20 [1.52–3.50]; patella 0.35–0.70 [0.40–0.70]; basitibia 1.60–3.00 [1.20–3.15]; distitibia 1.00–1.60 [0.80–1.65]; metatarsus + tarsus 0.95–1.60 [0.80–1.75].

Remarks.—*Sarax willeyi* was described by Gravely (1915) based on two specimens collected by Dr. A. Willey in New Britain, which were stated to be in the Indian Museum in Calcutta. Pocock (1898) examined the specimens collected by Dr. A. Willey in New Britain, compared them with *Sarax* specimens from Luzon Island and Andaman Islands, and having agreed with Kraepelin (1895), he concluded that only the single species, *S. sarawakensis*, was recognized in *Sarax*. Although Gravely (1915) did not refer to Pocock (1898), the specimens collected by Dr Willey in New Britain that they examined may have been the same.

Gravely (1915) distinguished *S. willeyi* from *S. sarawakensis* by the proximal spine of the pedipalpal tarsus being more than half as long as the distal one (less than half in *S. sarawakensis*). The specimens from Batanta Island, Salawati Island, and Madang in Papua New Guinea that we examined have the proximal spine of the pedipalpal tibia longer than half the length of the distal spine. The holotype of *Charon sarawakensis* (= *Sarax sarawakensis*), on the other hand, has the pedipalpal tibia with the proximal spine shorter than half the length of distal one. In addition, the holotype of *C. sarawakensis* has the pedipalpal tarsus armed with two very small denticles, while all of our specimens identified as *S. willeyi* have the pedipalpal tarsus with two rather long denticles. All the distribution records of *S. sarawakensis* in the Papuan regions including Solomon Islands and Bismarck Archipelago, such as reported by Kraepelin (1899), need reconfirmation. At this moment, it is reasonably considered that *S. sarawakensis* is restricted, in its distribution, to the Oriental region.

Natural history.—We found this whip spider most often under stones, and when specimens were collected during the day, they were found in a resting position attached to the underside of a stone on forest floor. We also collected some individuals under fallen trees in Salawati Island. According to the collection data, the specimens from Madang, Papua New Guinea were collected under rotten logs.

Distribution.—This species occurs in New Britain (Gravely 1915), and is here newly recorded from the West Papua Province of Indonesia, and in the Madang Province of Papua New Guinea (Fig. 5).

Sarax newbritainensis new species
(Figs. 1b, 3a–h)

Type material.—Holotype male, Papua New Guinea, East New Britain Province, New Britain Island, Resurgence Lali Bairaman (GPS coord. aprox. 05°39′32.59″S, 151°12′39.91″E), 17 February 2005, R. Sougeat (Expé Papou 2005)

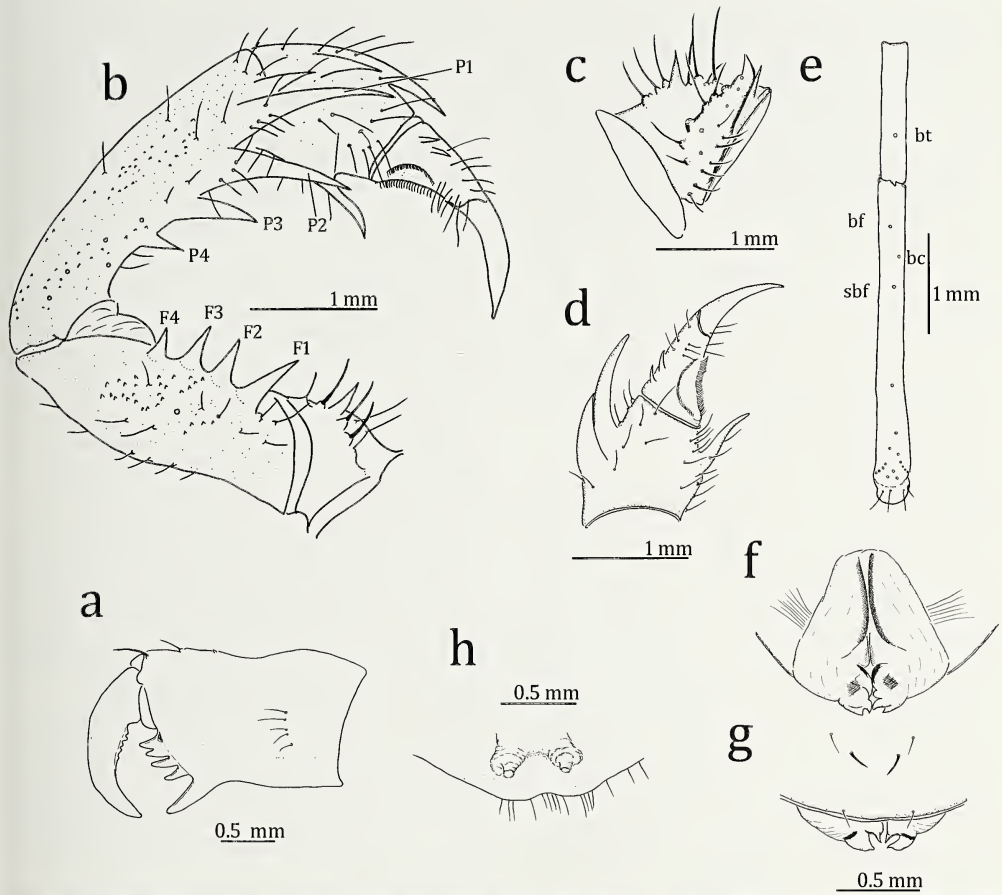

Figure 3.—*Sarax newbritainensis*, new species, from New Britain, Papua New Guinea. a. External view of left chelicerae; b. Antero-dorsal view of left pedipalp; c. Antero-ventral of left pedipalpal trochanter; d. Left pedipalpal tibia; e. Arrangement of trichobothria on fourth basitibial segment and distibia of left leg IV; f, g. Male genitalia (f. dorsal view; g. ventral view); h. Dorsal view of female gonopods.

(MNHN.Am.6). Paratype: 1 female, same locality data as the holotype (MZB.Ambl.134).

Etymology.—The specific name refers to the island where the type locality is located.

Diagnosis.—*Sarax newbritainensis* differs from all other congeneric species in the region by the large adult body length (about 8.25–9.5 mm) and the pale brown body. The carapace is proportionally less wide, without distinct lateral sulci, and the eyes are reduced in size. The pedipalpal tarsus has two rather long denticles, separated from each other by about twice the basal diameter of the denticle; the proximal denticle is about half as long as the distal one. The legs are elongate; metatarsi of leg II–IV are longer than the length of the subsequent three tarsal segments combined. Tibia of leg IV with 19 trichobothria, arranged with *bc* situating near the middle of *bf* and *sbf* and *bt* close to the distal margin of the fourth basitibial segment.

Description.—*Male:* Color in alcohol: Carapace light brown with darker marks; pedipalps brown but pedipalpal tarsus light brown. Legs I–IV yellowish brown, without annulations except for tibia and tarsus of leg I having white annulations; patella dark brown.

Carapace (Fig. 1b): Width about 1.3 times the length; surface finely granulate, sparsely with small tubercles, without setiferous tubercles; sulcus deep and distinct on posterior one-fourth of carapace. Flange present from level of lateral eyes to posterior margin, wide and bent upward along lateral margin, narrow on posterior margin. Anterior margin of carapace

rounded, with six frontal setae and four small fine setae close to each antero-lateral corner; slightly concave in part anterior to lateral eyes. Median eye tubercle black, without apical seta, slightly reduced in size, slightly emarginated antero-medially to form heart shape; eyes facing antero-laterally. Lateral eyes close to lateral margin of carapace, distance between them about the diameter of the lateral eye, normal pigmentation and tapetum. Frontal process triangular, visible from above.

Chelicera (Fig. 3a): Dorsum smooth, with three setiferous tubercles and two fine frontal setae. Basal segment with four teeth: the lowermost tooth largest, the uppermost tooth bicuspid, with upper cusp larger than lower cusp; inner surface with 14 setae arranged in vertical row near proximal margin; outer surface with small blunt tooth opposite the bicuspid tooth, and with five setae arranged in vertical row. Movable hand with five teeth; second tooth largest.

Sternum: First sternite (= tritosternum) elongate, with paired apical and strong median setae, five setae between apical and median setae and 12 small setae at base. Second and third sternites rounded, with paired apical setae; second with six basal setae; third with five basal setae.

Pedipalp (Figs. 3b–d): Short and stout, with several setiferous tubercles. Trochanter with a row of seven setiferous tubercles on antero-dorsal margin, six setiferous tubercles dorsally and one median spine on antero-ventral margin, medially with one spine and eight setiferous tubercles; ventral anterior apophysis equipped with several setiferous tubercles in basal part present on distal margin of trochanter (Fig. 3c). Femur with four major spines, several setiferous tubercles and small tubercles on antero-dorsal part, length of spine F1>F2>F3>F4; four major spines, several setiferous tubercles and small tubercles on antero-ventral margin, one spine present dorsally of FI and as long as 3/4 length of FI, length of spine FI>FII>FIII>FIV, one minor spine between FI and FII. Patella with four major spines, several setiferous tubercles and small tubercles on antero-dorsal margin, length of spine P1>P2>P3>P4; one setiferous tubercle and one spine between P1 and distal margin of patella, the spine as long as half length of P1; three major and one minor spines, several setiferous tubercles and small tubercles on antero-ventral margin, length of spines PI>PII>PIII. Tibia with two major spines on antero-dorsal margin, length of proximal spine more than half the length of distal one (Fig. 3d); antero-ventral margin with one major spine; outer surface finely granulate, with several setiferous tubercles. Tarsus completely divided (claw clearly demarcated by articulation), with two denticles on antero-dorsal margin: proximal denticle slightly longer than half the length of distal one, distance between them about three times basal diameter of proximal denticle; cleaning organ ventrally with 28–30 modified hairs; several blunt setae on inner surface of tarsus; apotele present.

Legs (Fig. 3e): Femora of Legs IIV with small setiferous tubercles. Tibia and tarsus of leg I with 23 and 41 segments, respectively; tibiae of leg II and III two-segmented; basitibia of leg IV four-segmented: fourth segment with one trichobothrium (value in parentheses as for *S. willeyi*), *bt* (0.57); distitibiae of Legs II–IV with 18 trichobothria, *bf* (0,13), *sbf* (0.32), *bc* (0.23), *bt* close to distal margin, *bc* at the middle of *bf* and *sbf*, (Fig. 3e). Tarsi of Legs II–IV four-segmented; first segment slightly longer than length of subsequent three segments combined; second segment with light yellow transverse line; fourth segment without oblique slit; pulvilli present.

Genitalia (Figs. 3f, g): Covered ventrally by genital operculum, of which posterior margin is equipped with paired setae; posteriorly with paired ventral and dorsal lobes, the dorsal lobe smaller than ventral one (Fig. 3f). In dorsal view, submedian brown bands running from anterior margin to the middle; inner margin of median lobe with brown region weakly sclerotized; brown spot present on each median lobe. In ventral view, base of ventral lobe with a narrow brown band (Fig. 3g).

Female: Similar to the male but differing as follows: carapace slightly darker; chelicera with three frontal fine setae; meta-sternum slightly more elongate, with two apical setae; tibia and tarsus of leg I respectively with 26 and 42 segments. Gonopods soft, cone-shaped, with several setae on margin of genital operculum (Fig. 3h).

Measurements.—Male (holotype, MNHN.Am.6) [female (paratype, MZB.Ambl.134)]; values for segments of the appendages are their lengths: Body length (excluding chelicera) 9.50 [8.25]. Carapace: median length 3.75 [3.50], width 5.00 [5.00]; median eye to anterior margin 0.05 [0.05], distance between lateral eyes 2.60 [2.25], lateral eye to anterior margin 0.60 [0.65], lateral eye lateral margin 0.20 [0.25]. Pedipalps: trochanter 1.00 [1.15], femur 3.20 [2.50], patella 3.25 [3.00], tibia 1.50 [1.25], tarsus 1.60 [1.50]. Leg I: femur 10.00 [10.15], patella 0.75 [0.75]. Leg II: femur 6.00 [5.75], patella 1.00 [1.00], basitibia 5.00 [4.90], distitibia 3.00 [2.90], metatarsus+tarsus 2.55 [2.60]. Leg III: femur 7.25 [6.50], patella 1.10 [1.25], basitibia 6.35 [6.25], distitibia 3.50 [3.25], metatarsus+tarsus 2.95 [3.00]. Leg IV: femur 6.50 [5.75], patella 1.00 [1.00], basitibia 7.25 [6.75], distitibia 2.95 [2.75], metatarsus+tarsus 3.00 [3.00].

Remarks.—*Sarax newbritainensis* is distinguished from the other *Sarax* species known from New Britain, *S. willeyi*, by the generally larger body, the distinctly paler coloration, the carapace proportionally less wide (about 1.3 times as wide as long, while about 1.5 times in *S. willeyi*) and without distinct lateral sulci, the eyes reduced in size, the strongly elongated legs, and the number and arrangement of the trichobothria as given in the key.

Natural history.—We collected the specimens of *S. newbritainensis* from the caves called Resurgence of Lali Bairaman in New Britain. The species has characteristics typical of cave dwellers such as small eyes, elongate legs, and pale body color.

Distribution.—This species is known only from the type locality in New Britain (Papua New Guinea) (Fig. 5).

Sarax monodenticulatus new species
(Figs. 1c, 4a–h)

Type material.—Holotype male, Indonesia, West Papua Province, Waigeo Island, Mumes (00°21.23′S, 130°58.93′E), under stone in limestone forest, Raja Ampat Regency, 10 June 2007, C. Rahmadi, E-Win 2007 LIP1 (MZB.Ambl.135). Paratypes: 1 female (MZB.Ambl.136), 1 male (MNHN.Am.7), 2 juveniles (MZB.Ambl.140), same data as holotype; 4 males (MZB.Ambl.137, 138, 141, 143), 3 females (MZB.Ambl.139, 142,144), Air Dingin Monfaya (Resurgence), Wairabiae Lopintol (00°18.13′S, 130°56.09′E), under stone in limestone forest, Raja Ampat Regency, 4 June 2007, C. Rahmadi.

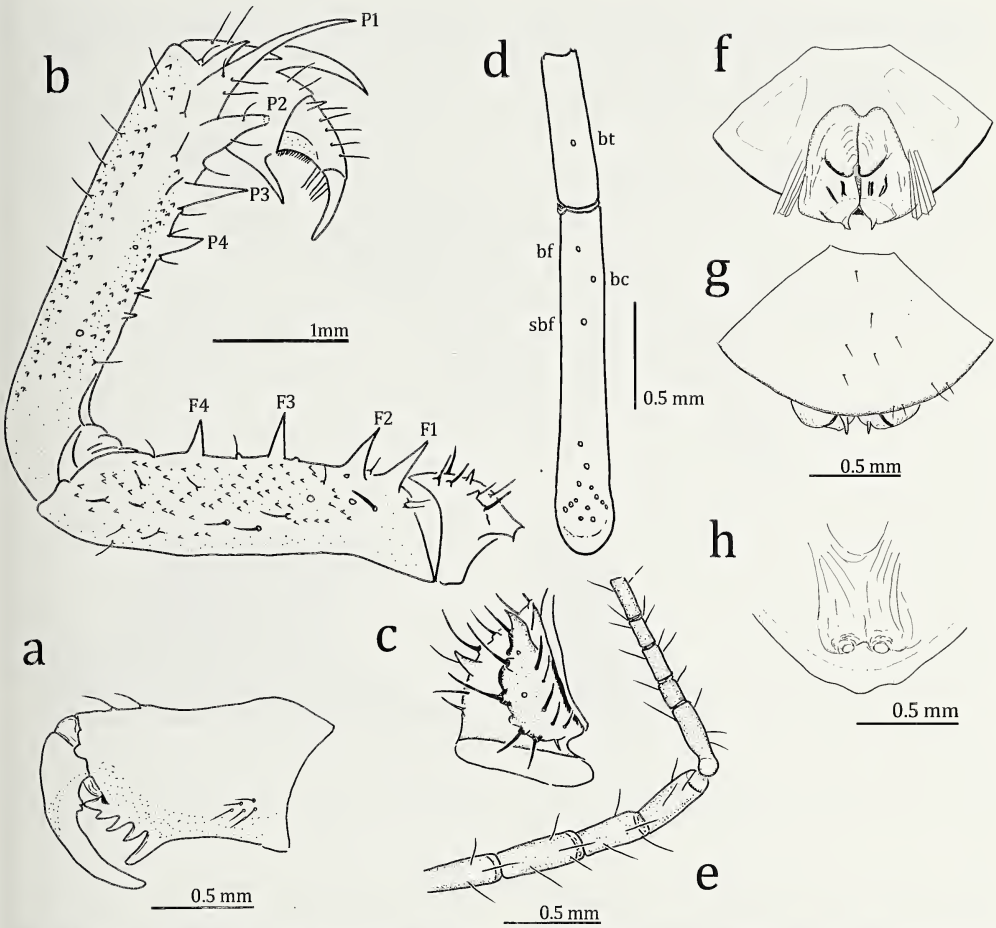

Figure 4.—*Sarax monodenticulatus*, new species, from Waigeo Island, Indonesia. a. External view of left chelicerae; b. Antero-dorsal view of left pedipalp; c. Antero-ventral view of left pedipalpal trochanter; d. Arrangement of trichobothria on fourth basitibial segment and distibia of left leg IV; e. Apical four tibial and basal five tarsal segments of antenniform leg I; f, g. Male genitalia (f. dorsal view; g. ventral view); h. Dorsal view of female gonopods.

Etymology.—The specific name refers to the presence of one denticle on the pedipalpal tarsus.

Diagnosis.—*Sarax monodenticulatus* differs from other congeneric species in the region by being small- to medium-sized (adult body length 2.5–6.5 mm) and with a reddish-brown carapace. The pedipalpal tarsus has a single denticle. Metatarsus of leg I as long as the subsequent two segments together; short- and long-segment alternating combination present in second to eleventh tarsal segments.

Description.—*Male:* Color in alcohol: Carapace dark reddish-brown with darker marks; pedipalp dark brown but pedipalpal tarsus light brown. Legs I–IV brown, without annulations, but tibia and tarsus of leg I yellowish brown, with white annulations. Basitibiae of Legs II–IV brown; their distibiae and tarsi greenish-brown. Abdomen dark brown; each tergite with yellow marginal line and light-brown spots.

Carapace (Fig. 1c): Width about 1.5 times its length; surface finely granulate; frontal area with dense, small tubercles, without setiferous tubercles; median sulcus present in posterior one-fourth of the carapace. Flange present in area posterior to lateral eyes, wide but narrow in posterior margin, bent upward. Anterior margin of carapace rounded, with six

frontal setae and some fine setae close to antero-lateral corner. Median eye tubercle black, without apical setae, slightly emarginated antero-medially to form heart shape; eyes facing antero-laterally. Lateral eye large, with normal pigmentation and tapetum, separated from lateral margin of carapace by about its diameter. Frontal process triangular, visible from above.

Chelicera (Fig. 4a): Dorsum smooth, with two fine frontal setae and several setae on dorsal and lateral parts of outer margin. Basal segment with four teeth: lowermost tooth largest, uppermost tooth bicuspid, with upper cusp larger than lower one; inner surface with eight setae arranged in a vertical row close to proximal margin; outer surface with a small blunt tooth and five setae near proximal margin. Movable hand with two teeth close to the proximal margin.

Sternum: First sternite (= tritosternum) elongate, with paired apical and median setae, paired small setae between apical and median setae, and four small setae basally. Second and third sternites rounded, each with paired apical setae.

Pedipalp (Figs. 4b, c): Strong and slender, with several setiferous tubercles and small tubercles. Antero-dorsal margin of trochanter with four setiferous tubercles dorsally, two spines and seven setiferous tubercles ventrally; antero-ventral margin with ventral anterior apophysis basally equipped with several setiferous tubercles; ventral anterior apophysis with one spine medially and one spine dorsally (Fig. 4c). Femur with four major spines, several setiferous tubercles and small scales on the antero-dorsal margin, length of spine F1>F2>F3>F4; five major spines, two minor spines, four setiferous tubercles and small scales present on antero-ventral margin, one spine present dorsally of FI and about as long as 3/4 length of FI, length of spine FI>FII>FIII>FIV, single minor spine present between FII and FIII and between FIII and FIV. Patella with four major spines, several setiferous tubercles and small scales on antero-dorsal margin, length of spine P1>P2>P3>P4, one minor spine present between distal margin and P1 and as long as half of the length of P1, two spines and ons setiferous tubercle present between P4 and the proximal margin; three major spines and one minor spine, several setiferous tubercles and small scales on antero-ventral margin, length of spine PI>PII>PIII, one minor spine between PIII and the proximal margin. Tibia with two major spines on antero-dorsal margin: proximal spine slightly longer than half of distal one; one major spine on antero-ventral margin close to distal margin; outer surface finely granular, with setiferous tubercles arranged in three rows. Tarsus completely divided (claw clearly demarcated by articulation), with one denticle on antero-dorsal margin; blunt setae present on inner surface; cleaning organ ventrally with 27–28 modified hairs; apotele present.

Legs (Figs. 4d, e): Femora of Legs I–IV with small scales and setae forming a longitudinal row. Tibia and tarsus of leg I with 23 and 41 segments, respectively (Fig. 4e); tibiae of legs II–III two-segmented; basitibia of leg IV four-segmented (in some specimens left basitibia three-segmented): fourth (third in specimen with three basitibial segments) segment with one trichobothrium (value in parentheses as for *S. willeyi*) *bt* (0.61); distitibiae of legs II–IV each with 16 trichobothria (Fig. 4d), *bf* (0.10), *sbf* (0.30), *bc* (0.17), *bc* about the middle of *bf* and *sbf*, *bt* close to distal margin. Tarsi of legs II–IV four-segmented; first segment about as long as length of the subsequent three segments combined; second segment with light yellow transverse line; fourth segment without oblique slit; pulvilli present.

Genitalia (Figs. 4f, g): Covered ventrally by genital operculum equipped with several setae; distally with paired small submedian lobes. In dorsal view, with paired large median lobes, of which distal margins are brown; four longitudinal sclerotized bands present posterior to median lobes (Fig. 4f). In ventral view, brown band present near base of distal lobe (Fig. 4g)

Female: Similar to the male. Gonopods soft and cone-shaped (Fig. 4h)

Measurements.—Male (n = 5) [female (n = 4)]; values for segments of the appendages are their lengths: Body length (excluding chelicera) 4.88–6.48 [2.48–5.60]. Carapace: median length 1.88–2.60 [2.00–2.48], width 2.60–3.72 [3.00–3.60]; median eyes to anterior margin 0.04–0.08 [0.04–0.08], distance between lateral eyes 1.20–1.80 [1.40–1.72], lateral eye to anterior margin 0.28–0.44 [0.36–0.40], lateral eye to lateral margin 0.12–0.16 [0.08–0.16]. Pedipalps: trochanter 0.40–1.00 [0.60–0.80], femur 1.20–3.08 [1.40–2.20], patella 1.40–3.52 [1.60–2.64], tibia 0.60–1.20 [0.68–1.00], tarsus 0.08–1.12 [0.60–1.20]. Leg I: femur 3.08–5.40 [3.40–4.80], patella 0.52–0.60 [0.40–0.48]. Leg II: femur 2.00–3.40 [2.40–3.20], patella 0.48–0.64 [0.48–0.72], basitibia 1.36–2.40 [1.60–2.40], distitibia 1.12–1.60 [1.20–1.60], metatarsus+tarsus 1.00–1.60 [1.20–1.36]. Leg III: femur 2.40–4.00 [2.80–3.60], patella 0.48–0.72 [0.56–0.60], basitibia 1.88–3.32 [1.88–3.00], distitibia 1.20–1.80 [1.36–1.68], metatarsus+tarsus 1.20–1.60 [1.20–1.44]. Leg IV: femur 1.20–3.48 [2.40–3.28], patella 0.60–2.80 [0.44–0.60], basitibia 0.48–3.20 [2.16–3.04], distitibia 1.40–2.80 [1.40–1.60], metatarsus+tarsus 1.04–1.80 [1.20–1.52].

Remarks.—This species is the only Papuan *Sarax* with a single denticle on the pedipalpal tarsus. The other *Sarax* species that have the single denticle on the pedipalpal tarsus are *S. javensis* (Gravely 1915) distributed in West Java and *S. cochinensis* (Gravely 1915) known from the Western Ghats in Cochin, India. Gravely (1915) distinguished the two species by the length of the denticle; the denticle of *S. cochinesis* is long and distinct, while in *S. javensis* it is minute (see Gravely 1915:figs. 2, 3). *Sarax monodenticulatus* is distinguished from these two species by having four-segmented basitibia (single- or two-segmented in *S. cochinensis* and three-segmented in *S. javensis* [see Gravely 1915:437]).

Natural history.—We collected specimens of this species mostly singly under stones in limestone forests. During the exploration of cave fauna in Waigeo Island, it was never found within the caves.

Distribution.—*Sarax monodenticulatus* is known only from Waigeo Island (Indonesia) (Fig. 5).

DISCUSSION

The first record of whip spiders of the genus *Sarax* from New Guinea was by Kraepelin (1895), who reported specimens without giving any precise data under the name *S. sarawakensis*, which was originally described from Borneo by Thorell (1888). Kraepelin (1895) also treated *S. brachydactylus* Simon 1892 described from Luzon Island, the Philippines, as a synonym of *S. sarawakensis*. Pocock (1898) recorded *S.*

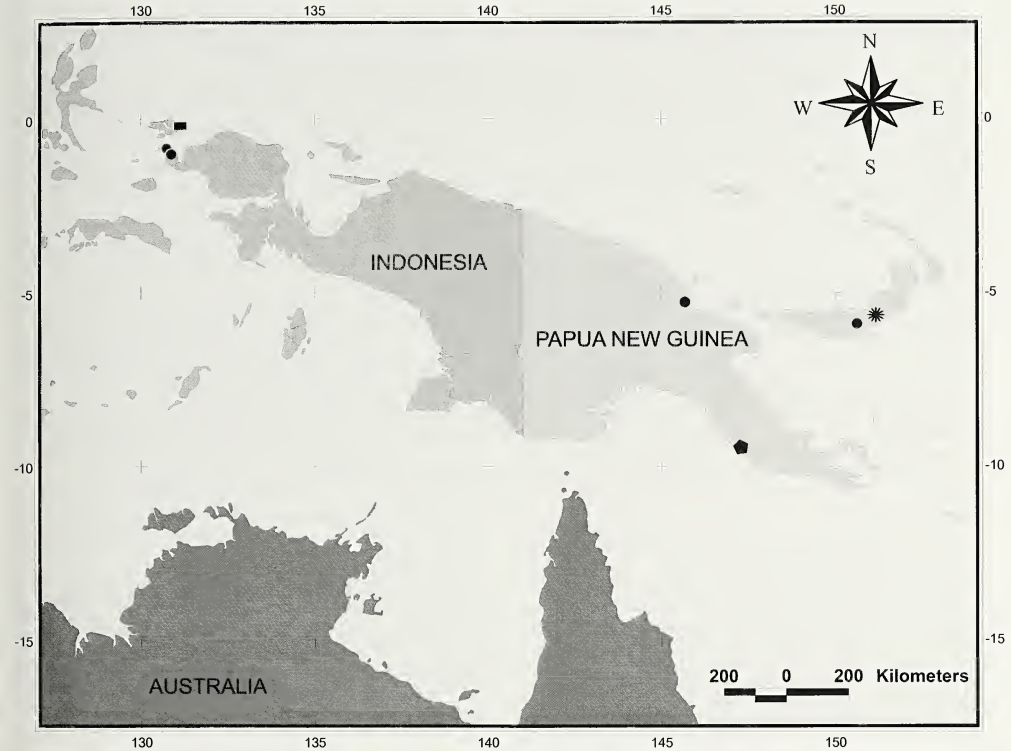

Figure 5.—Map showing the distribution of charinid species in the Papuan region. Symbols used: circle, *Sarax willeyi* from Batanta Island, Salawati Island (Indonesia), Madang and New Britain (Papua New Guinea); flower, *Sarax newbritainensis*, new species from New Britain; rectangle, *Sarax monodenticulatus*, new species from Waigeo Island (Indonesia); polygon, *Charinus papuanus* from Port Moresby (Papua New Guinea).

sarawakensis from New Britain and, following the view of Kraepelin (1895), remarked on its occurrence in Borneo, the Philippines, and New Guinea. Gravely (1915), on the other hand, described a species from New Britain as distinct from *S. sarawakensis* under the name *Salax willeyi*, possibly based on the specimens that Pocock (1898) identified as *S. sarawakensis* (see remarks in the section of *S. willeyi*). Consequently, the occurrence of *S. sarawakensis* in the Papuan region needs reconfirmation. Among the specimens from the Papuan region we have so far examined, we have not recognized any specimens of *S. sarawakensis*.

Sarax newbritainensis is very similar to *S. willeyi*, but can be distinguished from *S. willeyi* by the number and arrangement of the trichobothria. Compared with *S. willeyi* and *S. monodenticulatus*, both of which live outside caves, *S. newbritainensis* is larger in adult body size, has a pale body color, smaller median and lateral eyes, and strongly elongate legs, all characteristics highly adapted to cave environments. Such troglomorphic features have not so far been reported amongst *Sarax*, while several species of a similar genus, *Charinus*, are known to have such features (Baptista & Giupponi 2002; Weygoldt et al. 2002; Weygoldt & Van Damme 2004).

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read an earlier draft of the manuscript and provided us with comments and suggestions to improve the manuscript.

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Ontogeny repeats phylogeny in *Steatoda* and *Latrodectus* spiders

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Abstract. Web designs of young spiders are often less derived than those of older conspecific individuals. This study tested whether this "ontogeny repeats phylogeny" pattern occurs in two species of *Latrodectus* and two species of the closely related genus *Steatoda*. This pattern was assumed to occur in a recent study of a third *Latrodectus* species, *L. geometricus*, which attempted to deduce a probable evolutionary derivation of gum-foot webs of theridiids on the basis of ontogenetic changes. We found the same basic ontogeny repeats phylogeny ontogenetic pattern in all four species, suggesting that the previous suppositions were justified. As expected, the webs of the young instars of the two *Latrodectus* species were more similar than those of the adults, and were more similar to those of young than to those of adults of *L. geometricus*. One apparently derived trait of *L. mirabilis*, attaching prey remains as camouflage for the spider in the central portion of the web, did not change during ontogeny, and was present in even the webs of first-instar spiderlings. Field observations of *L. mirabilis* suggest that the ontogenetic change from light to darker abdominal color patterns that occurs in many *Latrodectus* species may result from changes in selection for camouflage associated with ontogenetic changes in web designs and the spiders' resting sites. The webs of *Steatoda* also fit the ontogenetic pattern: at least some ontogenetic changes in both species involved younger spiders having less derived traits than those of adults. The webs of young *Steatoda* spiders were more derived in some respects than those of the early instars of *Latrodectus*.

Keywords: Web design, ontogenetic pattern, plesiomorphic traits, web evolution

Morphological parallelism between ontogeny and phylogeny in numerous organisms seems to support the Biogenetic Law, which states that ontogenetic stages of a descendant tend to trace the phylogenetic history of adult ancestors (Eldredge and Cracraft 1980, review in Richardson and Keuck 2002). Similar patterns in behavioral features are scarce (Rial et al. 1993; Wenzel 1993). However, ontogenetic changes in the designs of spider webs are well known to show a "biogenetic" pattern in which the designs of the webs of younger individuals of a species tend to be more plesiomorphic than those of older individuals in those species in which web design changes as spiders mature. This pattern has been observed in 13 different web-building spider genera with different web designs (summaries in Eberhard 1990; Eberhard et al. 2008a; Kuntner et al. 2008, 2010). It is not clear why this pattern should occur, but it is so consistent that it was used "in reverse" in a recent study of the theridiid *Latrodectus geometricus* C.L. Koch 1841 to deduce the probable ancestral web form for theridiids on the basis of ontogenetic changes. This led to a reconstruction of the possible sequence of events leading to the abandonment of the ancestral orb web design in the evolutionary line of theridiids (Eberhard et al. 2008a). The webs of early-instar *L. geometricus* nymphs (but not those of the adults) have a clear radial organization of lines in the central area of the web, and the more or less regularly spaced lines bearing sticky silk are attached to these radial lines. In addition, the interior of the dense, central "disc" where the radial lines converge sometimes has a radial organization. Eberhard et al. (2008a) argued that these radial lines may be homologous to the radial and hub lines in orb webs, and that some details of the behavior used by *L. geometricus* to build radial and gumfoot lines may be homologous with traits associated with radius and sticky spiral construction of aranoid orb-weavers.

The present study asks whether this admittedly ambitious use of the ontogeny repeats phylogeny pattern of behavior was justified. We studied ontogenetic changes in the web designs of four additional species related to *L. geometricus*, two in the genus *Latrodectus* and two in its sister genus *Steatoda* (Agnarsson 2004). Using largely qualitative data, we asked two questions. Do the webs of younger individuals resemble more closely those of first-instar *L. geometricus* than they do those of older individuals of this species, as would be expected from previous studies? And do these ontogenetic differences involve younger spiders making more ancestral web designs?

The genera *Latrodectus* and *Steatoda* are part of a monophyletic line thought to have branched early from the rest of Theridiidae (Agnarsson 2004; Arnedo et al. 2004). Within the genus *Latrodectus*, *L. mirabilis* (Holmberg 1876) and *L. hesperus* Chamberlin and Ivie 1935 are part of one branch of the most basal bifurcation, while *geometricus* is in the other branch (Garb et al. 2003).

METHODS

Egg sacs of *L. mirabilis* were found associated with mature females collected on 12 December 2008 at Piedras de Afilar, Canelones, Uruguay (34°45′S, 55°33′W); one egg sac of *L. hesperus* (?) was collected in January 2009 in the Sonoran desert near Phoenix, Arizona, USA, from a web in which the female was inaccessible. Egg sacs were obtained from mature females of *Steatoda* nr. *hespera* Chamberlin & Ivie 1933 collected in December 2008 on Cerro San Bernardo at the northern edge of Salta, Argentina, and from *S. grossa* (C.L. Koch 1838) collected indoors in December in Montevideo, Uruguay. Unless stated otherwise, the descriptions below of webs of first-instar spiders refer to the first web built by the spiderling after it was removed from the cluster of individuals following its emergence from the

egg sac. We use the terms "nymph 1" and "first-instar nymphs" interchangeably to refer to the nymphal stage that emerges from the egg sac and builds a web (Foelix 1996).

Specimens of *S.* nr. *hespera* were identified by Ingi Agnarsson. The probable identities of *S. grossa* and *Latrodectus mirabilis* were deduced from the fact that they are the only species of these genera known to occur near Montevideo. Similarly, the most common species near Phoenix, Arizona is *L. hesperus*; nevertheless, *L. mactans* may also be present, and it is not possible at present to confidently identify even adults of these *Latrodectus* species (J. Miller pers. comm.). We thus refer to this species throughout as *L. hesperus* (?). Voucher specimens have been deposited in the arachnological collection of Facultad de Ciencias, Montevideo, Uruguay (*L. mirabilis* and *S. grossa*), in the Museo Argentino de Ciencias Naturales in Buenos Aires, Argentina (*S.* nr. *hespera*), and in the Museo de Zoología of the Universidad de Costa Rica (all species).

Spiders whose webs were to be photographed were placed in rectangular cardboard frames that were wrapped in fresh self-adhesive plastic wrapping material, to which the spiders almost never attached their lines. The dimensions of the frames varied with the size of the spider, from 8–10 × 6 × 5 cm for first-instar nymphs to 14 × 12 × 10 cm for adult female *S.* nr. *hespera*, *S. grossa*, and *L. hesperus* (?). Frame sizes for intermediate instar and adult *L. mirabilis* (12 × 12 × 14 cm) were based on dimensions of webs observed in the field. Webs were photographed before and after being coated with either talcum powder (early instars) or cornstarch (later instars and adults) (the finer grains of talcum powder provided better resolution of lines). In no case did we photograph or take data from more than one web of a given individual in any given instar. We attempted to mimic field conditions for some adult and first-instar *S.* nr. *hespera* by providing a cylindrical retreat in a sloping, moderately moist soil surface in a large container (30 × 16 × 8 cm for adults, a 8 cm diameter plastic cup for first instars) that was lined with paper and covered above with plastic wrap. In frames for larger individuals of *S. grossa* and *L. hesperus* (?), we included as a retreat a small cardboard tube slightly larger in diameter than the spider, in an attempt to more nearly mimic field conditions.

We concentrated on describing young webs (after only 1–3 nights of construction), in which early regularities in web construction had not yet been obscured by lines added later (Eberhard 1987; Benjamin & Zschokke 2002; Eberhard et al. 2008a). Webs were checked for the presence of masses of loose silk ("fluff") by careful searches of unpowdered webs under a dissecting microscope. The presence of sticky balls on lines was checked both by similar direct searches, and (in the case of young *S.* nr. *hespera*) by gently jarring lines throughout the web after powdering the web, thus removing the powder from non-sticky lines. The numbers of gumfoot lines attached to different horizontal lines were determined by searches in powdered webs under a dissecting microscope. The "length" of a horizontal line of this sort was taken to be the distance between attachments to other similar lines. The presence-absence of a central disc and the array of horizontal lines outside and inside the disc were determined by carefully searching in powdered webs under a dissecting microscope.

We analyzed presence-absence variables using Chi-square contingency tables and Fisher exact tests. Quantitative variables, maximum number of gumfoot lines attached to a single horizontal line and total number of gumfoot lines per web were analyzed with Mann-Whitney tests (*Z* approximation) or Kruskal-Wallis analyses of variance (*H*); pairwise comparisons were conducted using Mann-Whitney and Bonferroni corrections when the *H* value was significant.

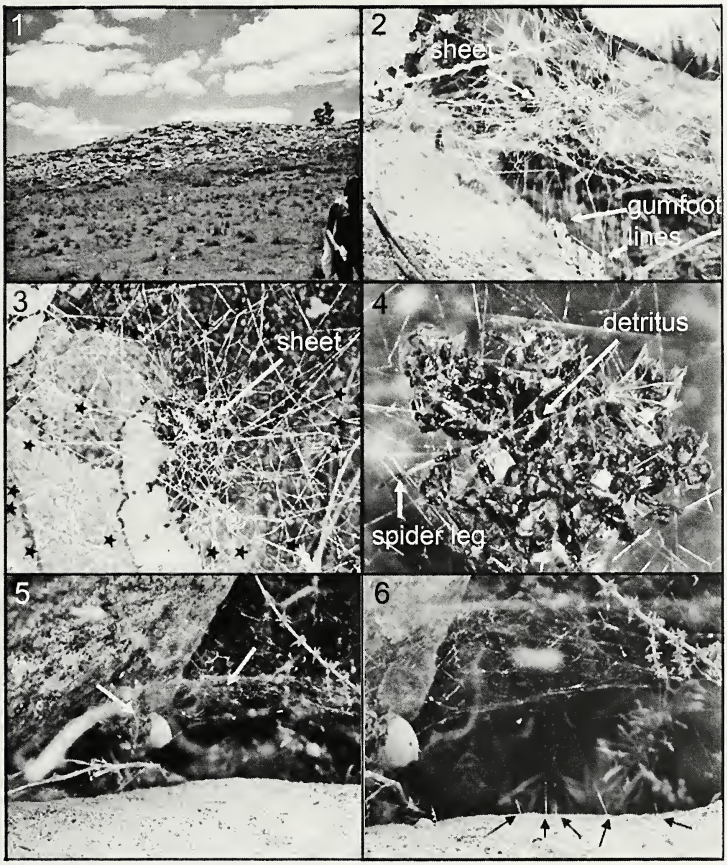
RESULTS

L. mirabilis.—*Field:* More than 300 webs of *L. mirabilis* ranging from those of 2nd instar nymphs to adults were observed in the field (Piedras de Afilar; Fig. 1). All of the webs of nymphs had a centrally located disc-like sheet in a tangle only a few cm above the surface of the ground (Figs. 2–4). In all cases the central disc had one (usually many more) body of apparent prey (nearly all ants) attached to it; some also had plant detritus. The spider rested under this "roof" of corpses, where it was difficult to discern visually (Fig. 4). At least some discs had more or less horizontal lines that seemed to radiate from their edges (lines with stars in Fig. 3). There were multiple vertical lines attached to the substrate below the web in some webs (Fig. 2); some lines appeared to have sticky silk at their lower tips.

In contrast, the webs of larger individuals (estimated 5th - penultimate instars) nearly always lacked accumulations of prey in the central portion of the web, and the spider rested at the edge of the web under an overhanging object (usually a rock) (Fig. 5). Some retreats had small accumulations of prey hanging near the undersurface of the rock, while others lacked prey carcasses entirely. One had vertical lines with sticky lower tips attached to the substrate below the horizontal sheet that extended from the site where the spider rested (Fig. 6). These spiders had darker abdomens (mostly black with red markings), thus contrasting with the light colors of early instars.

Captivity: Nymphs 1–3: The webs of ten first-instar nymphs built in captivity all had a central planar area (Table 1), where non-sticky, more or less horizontal lines with a distinct radial pattern converged (Figs. 7, 8). In eight of the webs this central area had a distinct disc-like sheet of more tightly meshed, non-sticky lines and in its interior also had lines with an at least vaguely radial organization (Figs. 7, 8). All webs had many (median 20, range 9–46) vertical or nearly vertical gumfoot lines attached below to the frame, each with a small sticky section about 1 mm long at its lower end. These were the only sticky lines seen in the web. The gumfoot lines were attached above to a more or less horizontal radial line, usually with a small white speck (fluff mass) at or near this attachment. These horizontal lines often had multiple, more or less regularly spaced vertical lines attached to them (median 3, range 2–5) (Fig. 7). None of the spiderlings had a retreat, and all remained at the central disc (Table 1). First-instar spiderlings fastened the remains of the first prey they captured close together at the central disc, thus producing small versions of the roof structures seen in the field.

Captivity: Late instar female nymphs and adult females: Nine webs (three of late juveniles and six of adult females) differed from those of first-instar nymphs in having a more clearly defined, domed, more or less horizontal sheet of non-sticky lines rather than a central disc, and in lacking a clear radial organization of lines in or around the sheet (Tables 1,



Figures 1–6.—Habitat and web traits in the field of late-instar *Latrodectus mirabilis*. 1. Outcrop of large rocks where different-instar *L. mirabilis* were very abundant. Spiders were most abundant near the crest of this hill. 2. Lateral view of nearly vertical gumfoot lines in a late instar web. 3. Approximately horizontal lines (black stars) converging at the center of the sheet (disc). 4. Close up of prey carcasses (mostly ants) attached to the center of the web under which the spider rests. 5. Spider retreat under an overhanging rock. An egg sac (spherical structure) indicates the site where the spider rests. 6. Sticky lower tips of gumfoot lines.

2). They also lacked the approximately horizontal lines from which multiple vertical gumfoot lines ran to the substrate below. All webs had multiple gumfoot lines attached to the substrate below, with a 1–3 mm portion at the very tip covered with sticky balls; no other sticky lines were seen in these webs. Webs of late juveniles and adults lacked silk retreats. All included an accumulation of prey remains in the central portion of the sheet, but they were scattered rather in a tight group as in younger spiders.

***L. hesperus* (?).**—*Captivity:* Nymph 1: The first webs of 23 first-instar spiderlings built in captivity were qualitatively indistinguishable from the webs of first-intar *L. geometricus* (Eberhard et al. 2008a: Table 1). They all had a small, central, more or less horizontal disc where the spider rested. In most cases (20 of 23), the horizontal lines that surrounded the disc had an approximately radial arrangement converging on the disc (Figs. 9, 10). All webs had approximately vertical gumfoot lines, which were attached to the floor of the frame and had balls of adhesive silk on the bottom 2–3 mm. No other lines in the web were sticky. Usually each gumfoot line had a small mass of fluff near its upper end where it was attached to the horizontal lines (arrows in Fig. 10). The fluff masses were presumably the reeled-up remains of the line that was removed as part of "cut and reel" behavior during the construction of the gumfoot lines (Eberhard et al. 2008a). The total number of gumfoot lines (median 30, range 6–45, $n = 23$

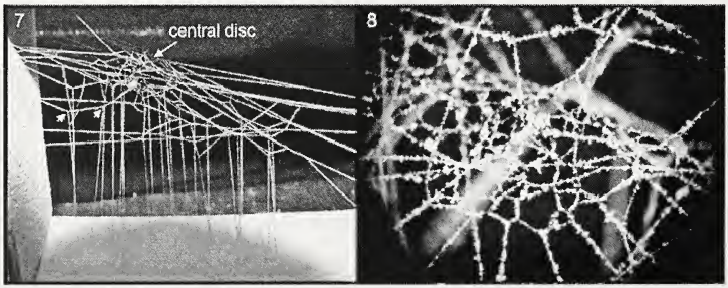
Table 1.—Comparisons of web traits of early juveniles and adults of five Theridiidae species: *Latrodectus mirabilis* (Lm), *L. hesperus* (Lh), *L. geometricus* (Lg) (Eberhard et al. 2008a), *Steatoda* nr. *hespera* (Sh), and *S. grossa* (Sg). (– trait absent in webs; ? trait not recorded in webs).

	edge (retreat)[1]	hub[2]	radii in hub[3]	gumfoot lines[4]	other sticky lines[5]	sheet[6]	sticky lines in sheet[7]	horiz[8]	fluff[9]	prey[10]
Latrodectus geometricus										
nymph 1	N	Y	SOME	Y	N	N	–	Y	Y	N
adults	Y	N	–	Y	N	Y	N	Y	Y	N
mirabilis										
nymph 1	N	Y	SOME	Y	N	N	–	Y	Y	Y
adults	Y	N	–	Y	N	Y	N	N	?	Y
hesperus (?)										
nymph 1	N	Y	SOME	Y	N	N	–	Y	Y	N
adults	Y(N)	N	–	Y	N	Y	N	N	FEW	N
Steatoda nr. *hespera*										
nymph 1	N	N (sheet)	–	Y	Y (tangle)	Y	N	FEW	FEW	N
adults	Y	N	–	Y	Y (tangle)	Y	N	?	?	N
grossa										
nymph 1	N	N	–	Y	N	Y	N	SOME	Y	N
adults	Y	N	–	Y	Y (tangle)	Y	N	FEW	FEW	N

[1] Spider resting at edge of web (distinct silk structure built in which it rests).
[2] More or less radial lines converging at central point ("hub" or disc) in midst of web.
[3] Perceptible radial organization of lines inside "hub".
[4] Gumfoot lines, which have relatively short segment coated with sticky material very near the tip where line is attached to substrate.
[5] Sticky material on other lines in web beside gumfoot lines.
[6] Discernable more or less horizontal sheet.
[7] Sheet including some sticky lines.
[8] Most gumfoot lines attached at top to a more or less horizontal line to which at least one other gumfoot line is attached.
[9] Top end of gumfoot line with small white mass of loose silk ("fluff").
[10] Prey carcasses attached to sheet. Spider generally rests under them where it is at least partly hidden.

webs) was lower than in *L. geometricus* webs (median 38, range 31–47, $n = 14$ webs; $H = 23.17$, $P = 0.00012$; Table 2). The lines within the central disc were only seldom (3 of 23) recognizably radial in orientation. Three webs had more than one disc (two with two, one with three), and in one web the single disc was elongate rather than circular. First-instar *L. hesperus* (?) spiderlings never attached their prey to the central disc (Table 2).

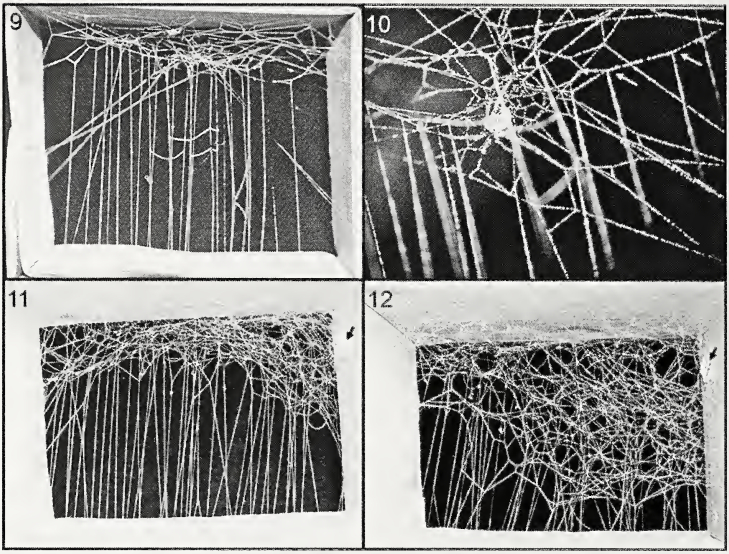
Captivity: Mature females: Nine adult females built webs in captivity. Six spiders occupied the tunnel in the frame; the other three rested in an upper corner of the frame but did not build a silk retreat at the resting place. None of the webs of adult females had any indication of the radial organization seen in the webs of first-instar nymphs. All nine webs had a sheet in the upper portion of the frame that varied in density from sketchy to moderately dense; the sheet slanted slightly downward from either the upper edge of the tunnel (Figs. 11, 12) or the resting place. Relatively straight "signal lines" ran to the near edge of the sheet from the upper edge of the tunnel or from the resting place of those spiders that did not rest in



Figures 7–8.—Characteristics of first-instar nymph of *Latrodectus mirabilis*. 7. Complete web of a first-instar nymph; arrows show two gumfoot lines attached to a single horizontal line. 8. Dorso-lateral view of the central disc under a dissecting microscope, showing the converging, approximately horizontal lines.

Table 2.—Quantitative comparison of web characteristics between first-instar nymphs (i1) and adult females of five Theridiidae species: *Latrodectus mirabilis* (Lm), *L. hesperus* (Lh), *L. geometricus* (Lg) (Eberhard et al. 2008a), *Steatoda* nr. *hespera* (Sh), and *S. grossa* (Sg). Same letters above species indicate statistical differences. Variables are defined in Table 1. (NA- not possible to apply a statistic test; Ø- no data available for the corresponding group).

Variable	Groups compared	Comparison	Values compared	Test	*P*
Retreat	i1/ad (Lm)	Yes-No	0/10, 0/9	NA	
	i1/ad (Lh)	Yes-No	0/23, 6/9	Fisher Exact	0.0001
	i1/ad (Lg)	Yes-No	0/15, 14/14	Fisher Exact	<0.00001
	i1/ad (Sh)	Yes-No	0/14, 6/9	Fisher Exact	0.0008
	i1/ad (Sg)	Yes-No	0/11, 10/11	Fisher Exact	<0.00001
	i1: Lm, Lh, Lg, Sh, Sg	Yes-No	0/10, 0/23, 0/15, 0/14, 0/11	NA	
	ad: Lm, Lh, Lg, Sh, Sg	Yes-No	0/9, 6/9, 14/14, 6/9, 10/11	$X^2_{(4)} = 28.96$	<0.00001
Circular disc	i1/ad (Lm)	Yes-No	10/10, 0/9	Fisher Exact	0.0001
	i1/ad (Lh)	Yes-No	23/23, 0/9	Fisher Exact	<0.00001
	i1/ad (Lg)	Yes-No	15/15, 0/14	Fisher Exact	0.0001
	i1/ad (Sh)	Yes-No	0/14, 0/9	NA	
	i1/ad (Sg)	Yes-No	0/11, 0/11	NA	
	i1: Lm, Lh, Lg, Sh, Sg	Yes-No	10/10, 23/23, 15/15, 0/14, 0/11	$X^2_{(4)} = 73.00$	<0.00001
	ad: Lm, Lh, Lg, Sh, Sg	Yes-No	0/9, 0/9, 0/14, 0/9, 0/11	NA	
Sheet	i1/ad (Lm)	Yes-No	0/10, 9/9	Fisher Exact	0.0001
	i1/ad (Lh)	Yes-No	0/23, 9/9	Fisher Exact	<0.00001
	i1/ad (Lg)	Yes-No	0/15, 14/14	Fisher Exact	0.0001
	i1/ad (Sh)	Yes-No	14/14, 9/9	NA	
	i1/ad (Sg)	Yes-No	11/11, 11/11	NA	
	i1: Lm, Lh, Lg, Sh, Sg	Yes-No	0/10, 0/23, 0/15, 14/14, 11/11	$X^2_{(4)} = 73.00$	<0.00001
	ad: Lm, Lh, Lg, Sh, Sg	Yes-No	9/9, 9/9, 14/14, 9/9, 11/11	NA	
Radial organization outside disc	i1/ad (Lm)	Yes-No	8/10, 0/9	Fisher Exact	0.0007
	i1/ad (Lh)	Yes-No	19/23, 0/9	Fisher Exact	<0.00001
	i1/ad (Lg)	Yes-No	15/15, 0/14	Fisher Exact	<0.00001
	i1/ad (Sh)	Yes-No	2/14, 0/9	Fisher Exact	0.50
	i1/ad (Sg)	Yes-No	0/11, 0/11	NA	
	i1: Lm, Lh, Lg, Sh, Sg	Yes-No	8/10, 19/23, 15/15, 2/14, 0/11	$X^2_{(4)} = 45.36$	<0.00001
	ad: Lm, Lh, Lg, Sh, Sg	Yes-No	0/9, 0/9, 0/14, 0/9, 0/11	NA	
Radii inside hub	i1/ad (Lm)	Yes-No	8/10, 0/9	Fisher Exact	0.0007
	i1/ad (Lh)	Yes-No	3/23, 0/9	Fisher Exact	0.99
	i1/ad (Lg)	Yes-No	8/15, 0/14	Fisher Exact	0.0022
	i1/ad (Sh)	Yes-No	0/14, 0/9	NA	
	i1/ad (Sg)	Yes-No	0/11, 0/11	NA	
	i1: Lm, Lh, Lg, Sh, Sg	Yes-No	8/10, 3/23, 8/15, 0/14, 0/11	$X^2_{(4)} = 31.75$	<0.00001
	ad: Lm, Lh, Lg, Sh, Sg	Yes-No	0/9, 0/9, 0/14, 0/9, 0/11	NA	
Other sticky lines	i1/ad (Lm)	Yes-No	0/10, Ø	NA	
	i1/ad (Lh)	Yes-No	0/23, 8/9	Fisher Exact	<0.00001
	i1/ad (Lg)	Yes-No	0/15, 0/14	NA	
	i1/ad (Sh)	Yes-No	7/8, 3/3	Fisher Exact	0.99
	i1/ad (Sg)	Yes/No	0/11, 11/11	Fisher Exact	0.0001
	i1: Lm, Lh, Lg, Sh, Sg	Yes-No	0/10, 0/23, 0/15, 7/8, 0/11	$X^2_{(4)} = 57.65$	<0.00001
	ad: Lh, Lg, Sh, Sg	Yes-No	8/9, 0/14, 3/3, 11/11	$X^2_{(3)} = 33.31$	<0.00001
Max. no. of gumfoot lines/ horizontal line	i1/ad (Lm)	Medians (range)	3 (2–5), Ø	NA	
	i1/ad (Lh)	Medians (range)	4 (2–9), 1 (1–2)	$Z_{(23,\ 9)} = 4.31$	0.00002
	i1/ad (Lg)	Medians (range)	5 (3–6), 2 (1–2)	$Z_{(14,\ 14)} = 3.97$	0.00007
	i1/ad (Sh)	Medians (range)	2 (2–2), Ø	NA	
	i1/ad (Sg)	Medians (range	2 (2–5), 1 (1–2)	$Z_{(11,\ 11)} = 3.58$	0.00034
	i1: Lm^a, $Lh^{a,b}$, $Lg^{a,c}$, $Sh^{a,b,c,d}$, $Sg^{b,c,d}$	Medians (range)	3 (2–5), 4 (2–9), 5 (3–6), 2 (2–2), 2 (2–5)	$H = 35.69$	<0.00001
	ad: Lh, Lg, Sg	Medians (range)	1 (1–2), 2 (1–2), 1 (1–2)	$H = 4.88$	0.09
No. gumfoot lines/web	i1/ad (Lm)	Medians (range)	20 (9–46), Ø	NA	
	i1/ad (Lh)	Medians (range)	30 (6–45), 28 (9–43)	$Z_{(23,\ 9)} = 0.63$	0.53
	i1/ad (Lg)	Medians (range)	38 (31–47), 23 (12–34)	$Z_{(12,\ 14)} = 3.50$	0.00047
	i1/ad (Sh)	Medians (range)	14 (8–30), Ø	NA	
	i1/ad (Sg)	Medians (range)	26 (10–36), 8 (2–23)	$Z_{(11,\ 11)} = 3.59$	0.00014
	i1: Lm^a, Lh^b, $Lg^{a,b,c}$, $Sh^{b,c}$ Sg^c	Medians (range)	20 (9–46), 30 (6–45), 38 (31–47), 14 (8–30), 26 (10–36)	$H = 23.17$	0.00012
	ad: Lh^a, Lg^b, $Sg^{a,b}$	Medians (range)	28 (9–43), 23 (12–34), 8 (2–23)	$H = 17.31$	0.00017



Figures 9–12.—First- and adult-instar webs of *Latrodectus hesperus* (?) 9. First-instar web with a small central disc. 10. Close up view of the central disc under a dissecting microscope, showing some approximately horizontal lines and two gumfoot lines attached to a single horizontal line (white arrows). 11. Adult web with slanted long sheet and relatively small lower tangle; black arrow pointing to the tunnel retreat. 12. Adult web with an extended lower tangle; black arrow pointing to the tunnel retreat.

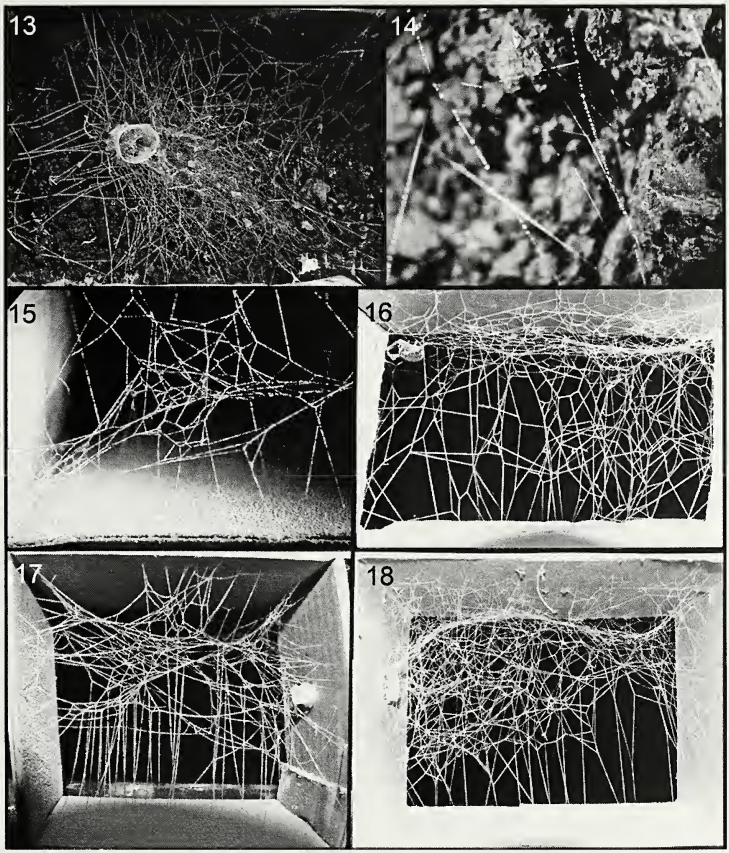
tunnels. A sparse tangle above the sheet was attached to the upper side of the cardboard frame. Six of the webs had a dense tangle below the sheet (Fig. 12), but in the other three webs this tangle was nearly absent. Short segments of threads of the tangle were coated with adhesive balls in eight webs. Numerous nearly vertical gumfoot lines ran from the periphery of the sheet to the frame floor (median 28, range 9–43, $n = 9$ webs), leaving an empty space just under the central portion of the sheet. Most gumfoot lines were attached individually at the top to threads in the sheet, or to a tangle line rather than to a horizontal line at the periphery of the sheet; only one web had two gumfoot lines attached to the same line. The sticky segment of these lines extended from nearly the bottom tip up to 10 mm (8.5 ± 1.8 mm, $n = 3$). Masses of silk fluff were only seldom seen near the upper ends of gumfoot lines. In some webs fluff may have been concealed by the dense tangle, but careful checks showed that the upper ends of many gumfoot lines lacked fluff masses. No prey remains were incorporated into webs.

Steatoda* nr. *hespera: *Field*: Four webs of mature female *S.* nr. *hespera* were found in the field near the ground on the steep slope of second-growth forest. Each spider rested in an approximately 8 mm diameter tunnel at the uphill edge of the web. A sparse, more or less horizontal sheet extended from the tunnel on the downhill side. Poor viewing conditions precluded determination of whether there were lines above and below the sheet.

Two mature females that were provided with a similar situation in captivity (a tunnel in a sloping bank of earth) built apparently similar webs (Fig. 13). The web had a moderately dense, horizontal sheet of irregularly oriented, non-sticky lines under which the spider moved very rapidly to chase and attack prey that were on the sheet and also on the ground below (they quickly wrapped and reeled in these prey, lifting them off the ground). Numerous lines laid near the soil (lines accumulated over many nights) had balls of glue that were visible when in a humid environment (Fig. 14); no clear pattern in the placement of these lines was discerned. Prey that had been consumed were dropped to the ground.

Captivity: Nymph 1: We photographed the first webs of 14 first-instar nymphs of *S.* nr. *hespera*, five after only a single night and nine after two nights in the frame. Web designs differed substantially in details, but they all shared several characteristics. All had at least some more or less vertical gumfoot lines (median 14, range 8–30; Fig. 15), and had an approximately horizontal, often elongate sheet of non-sticky silk. The spider rested on the sheet or at the edge of the web, but in no case did it build a silk retreat. There were at least some additional tangle lines above and below the sheet, but there was a space immediately below the sheet, thus giving the spider room to move freely. In only two cases did the lines around the edges of the sheet have a perceptible radial organization, but in no case did lines in the sheet have a perceptible radial pattern.

Several other traits varied. Only the tip of the line was covered with glue in most gumfoot lines, but some lines had glue along a substantial fraction of the line, and often lines attached to the frame floor had more than one sticky segment.



Figures 13–18.—Webs of *Steatoda* species. 13. Web of mature female *Steatoda* nr. *hespera* built in conditions mimicking those in the field. 14. Closeup view of early lines near the surface of the ground in a humid atmosphere, showing sticky balls on some but not other lines. 15. Web of first-instar nymph *S.* nr. *hespera* showing multiple gumfoot lines and a sparse sheet. 16. Web of mature female *S.* nr. *hespera* with a dense sheet built after three nights on a frame. 17. Web of first-instar nymph *S. grossa* with multiple gumfoot lines and relatively dense sheet. Nymph did not build a retreat inside the tunnel. 18. Web of mature female *S. grossa* showing a dense approximately domed sheet and its retreat inside the cardboard tunnel.

In most webs, gumfoot lines varied from nearly vertical to those that made much smaller angles (Fig. 15), and three webs had additional gumfoot lines running to the side of the frame. Gumfoot lines were generally attached individually to a more or less horizontal line in the tangle at the edge of the sheet; in only two webs were more than a single gumfoot line attached to the same horizontal line (Table 2). Most gumfoot lines lacked small accumulations of fluff at their upper ends. At least in seven of eight webs (in which this detail was checked) lines in the tangle (either above or below the central sheet) had stretches of glue on them. Prey remains were not incorporated in the web.

Captivity: Mature females: Three mature *S.* nr. *hespera* females built webs in frames that had an extensive sheet composed of irregularly oriented, non-sticky lines (Fig. 16). The sheet of one web was close to the top of the frame, while in the other two there was a loose tangle of lines above it. Two also had a loose tangle of lines below the sheet. Some lines in the tangle (above and below the sheet) were coated with sticky balls at several sites. Gumfoot lines were attached at their upper ends to a non-sticky line in the loose tangle below the sheet; others were attached to more or less horizontal sticky lines of the tangle. Some gumfoot lines had glue only near their lower tips, but in the rest the line was coated along nearly

its entire length with sticky balls (mean = 19.7, SD = 3.1, n = 3), except for a few mm (2–3 mm) at its very lower tip.

One of these females was observed building vertical sticky lines. Lines were not laid in bursts, but the spider returned to the retreat after attaching each line to the floor of the frame. In addition, it was clear that the spider did not cut and reel as it ascended after attaching one of these lines.

Steatoda grossa: *Captivity*: Nymph 1: Webs of 11 first-instar nymphs were photographed and examined. Nine webs had an upward sloping narrow sheet; the other two had a central, elongated disc. All webs had numerous vertical gumfoot lines (Table 2, Fig. 17), each with a short segment coated with sticky balls at its lower end where it was attached to the floor of the frame. The upper ends of most gumfoot lines were attached individually to short, more or less horizontal lines near the edge of the sheet (Table 2). In 62 of 85 gumfoot lines there was a discernible mass of fluff at or near this attachment. No other sticky lines were seen. There was no silk retreat where the spider rested in a corner of the cardboard frame at the top edge of the web. Nor was there any sign of radial organization within this sheet (or disc) or the lines around its margins (Tables 1, 2). Prey remains were not incorporated in the web.

Captivity: Adult females: The webs of ten females all lacked any indication of radial organization. Instead they had a dense, arch-shaped sheet composed of irregularly oriented non-sticky lines that ascended from the roof of the tunnel-retreat opening toward the top of the frame near the center and then descended toward the opposite side of the frame (Fig. 18). Dense tangles were present above and below the sheet in all webs. Lines of the tangle below were attached to the edge of the sheet, and the spider moved freely under the central portion of the sheet. In nine of the 10 webs short segments of some threads in the upper tangle were coated with sticky material; the other web had sticky segments in the tangle below the sheet. These lines with sticky segments were attached to other dry threads in the tangle with no apparent order or orientation. The number of gumfoot lines varied widely (median = 8, range 2–23, n = 10) and had sticky material covering up to the distal 17 mm (mean = 13.1 ± 2.5 mm, n = 9 lines). Most gumfoot lines were short, and many deviated substantially from being vertical. They were attached at their upper ends either to threads of the lower tangle or to the edge of the sheet. In only two webs did we see two gumfoot lines attached to the same thread (one case in each web). A fluff mass at the upper end was discernable in only a few gumfoot lines. Prey remains were not incorporated into webs.

DISCUSSION

Table 1 summarizes qualitative ontogenetic changes in web design in the four species of this study and in *L. geometricus*, while Table 2 gives quantitative comparisons among species and developmental stages. Some patterns were relatively general. In all five species the webs of first-instar nymphs lacked a retreat, while nearly all adult webs in four species had a retreat (Tables 1, 2). Only in *L. mirabilis* did adult webs in captivity lack a retreat, though the field webs of late-instar nymphs and adults had retreats under overhanging objects such as rocks. Possibly we did not provide these spiders with appropriate conditions to construct retreats in captivity.

The maximum number of gumfoot lines attached to a single horizontal line, as well as the total number of gumfoot lines per web, was higher in webs of first-instar nymphs than in conspecific adults in *L. hesperus* (?), *L. geometricus*, and *S. grossa* (Table 2) (data were not available for adult *L. mirabilis* and *S.* nr. *hespera*). First-instar nymphs of *L. geometricus* had the largest number of gumfoot lines per web (Table 2). Lines with sticky segments were present in the tangle web of first-instar nymphs of *S.* nr. *hespera* and adult *S.* nr. *hespera*, *L. hesperus* (?), and *S. grossa* (Tables 1, 2).

Some other ontogenetic patterns were more restricted. Those of *Latrodectus* were simpler so we discuss them first. The changes in *Latrodectus mirabilis* and *L. hesperus* (?) are very similar to those of *L. geometricus* (Eberhard et al. 2008a). Younger individuals of all three species differed from conspecific adults in producing *a*) a central planar area (disc), *b*) more or less radial lines around the disc, *c*) approximately horizontal lines near the disc to which multiple gumfoot lines were attached, *d*) larger numbers of gumfoot lines, *e*) webs lacking a more or less horizontal sheet and *f*) webs that lacked a silk retreat at the edge of the web or a retreat inside a tunnel (the spider instead rested under the central disc). In the webs of intermediate juvenile instars the central disc gradually became extended into a more elongate sheet, and the number of gumfoot lines attached to any given approximately horizontal line became smaller, as also occurred in *L. geometricus*. Independent evidence suggests that the traits of younger spiders with respect to *e* and *f* are ancestral compared with those of the adults (Eberhard et al. 2008a; Szlep 1965, 1968). One aspect of the ontogeny of *L. mirabilis* differed with *L. geometricus*: the first-instar nymphs and all later stages fastened the corpses of prey to the central disc or sheet, providing apparent camouflage for the spider.

Within *Steatoda*, *S.* nr *hespera* showed three ontogenetic changes in web design (younger spiders rested centrally on the web rather than at the edge, built a larger number of gumfoot lines and failed to build a retreat); in all of these respects the behavior of younger spiders is probably more ancestral (Eberhard et al. 2008a). In *S. grossa* two ontogenetic changes, the addition of sticky material to other lines in addition to gumfoot lines and the use of tunnel retreats in the webs of adults, also show the same pattern, the webs of adult spiders showing more derived web traits.

In general, the ontogenetic patterns in both genera thus fit with the tendency for web ontogeny to reflect phylogenetic changes in web design. These findings support the arguments made previously in attempting to deduce how gumfoot webs evolved from orbicular ancestral webs (Eberhard et al. 2008a, 2008b). Given our generally small sample sizes and the substantial variation in some web traits, the qualitative changes may be more certain than the quantitative changes. It is interesting to note that sticky silk may be particularly valuable to these spiders, as one mature female *S.* nr. *hespera* spent several minutes (possibly) re-ingesting sticky silk that she had wrapped onto a prey that subsequently escaped.

Comparing *Latrodectus* and *Steatoda*, independent evidence (Eberhard et al. 2008a) suggests that young *Steatoda* show more derived web traits than do young *Latrodectus*. The three traits accentuated in *Steatoda*, adding sticky material to lines other than gumfoot lines, discarding gumfoot lines, and

building a non-sticky sheet, are all thought to be more derived. The lack of gumfoot was apparent even on lines that ran more or less vertically to the substrate below in the webs of adult female *S.* nr. *hespera* built in cardboard frames, as they placed sticky balls not at the lower tips of these lines, but farther up away from the substrate. If the argument made previously (Eberhard et al. 2008a) that radial organization is an ancestral trait is correct, then a fourth trait, the lack of radial organization in the webs of first-instar *Steatoda*, is also derived.

The webs of young *Steatoda* resembled those of adult *Latrodectus* in that the lines to which gumfoot lines were attached above clearly lacked any radial organization, most of these approximately horizontal lines had only a single gumfoot line attached to them, and the web had an elongate, more or less planar sheet rather than a central disc even after only a single night of construction. In sum, the direction of change in *Steatoda* ontogeny was similar to that in *Latrodectus* (web designs of younger spiders were less derived), but the point of departure (the youngest *Steatoda* webs) was more derived in at least some respects than the point of departure for the *Latrodectus* species and was thus part way along the ontogenetic trajectory of *Latrodectus* species. After beginning by building webs similar to the webs of intermediate-sized *Latrodectus* (Eberhard et al. 2008a), *Steatoda* later produced webs that differed from those of any of the three *Latrodectus* species.

First-instar nymphs of all four species performed rapid attacks on prey, quickly reeling up the gumfoot line to which the prey had adhered and thus raising the prey rapidly from the substrate so that it was relatively helpless, then immediately wrapping it. These stereotyped and effective attacks (which in all species involved initiating wrapping with sticky silk) are well designed to function in webs with gumfoot lines (Barrantes & Eberhard 2007) and thus also fit the idea that gumfoot webs are ancestral in this group (Eberhard et al. 2008a, 2008b).

The webs of mature female *S.* nr. *hespera* and *S. grossa* contrast sharply with those described for adults of other species of *Steatoda*, some of which build typical gumfoot webs with one sheet (*triangulata*, *lepida*, *bipuncta*) (Nielsen 1931; Lamoral 1968; Benjamin & Zschokke 2002) (the sheet of *S. bimaculata* may also have sticky lines – Nielsen 1931) or two horizontal sheets and a tangle above with no sticky lines (*S. moesta*) (Eberhard et al. 2008b). The common tendency for adult web forms to diverge substantially among congeneric species in Theridiidae (Eberhard et al. 2008b) thus also holds for *Steatoda*. The web designs of individuals of *S.* nr. *hespera* were also especially flexible, comparing webs in cardboard frames with webs in more natural circumstances (Figs. 13, 16). Such intraspecific variation, previously documented in *Latrodectus* (Lamoral 1968; Kaston 1970), but not in *Steatoda*, is apparently also widespread in Theridiidae (Eberhard et al. 2008b). This variation makes it necessary to be cautious in generalizing from limited observations such as those we present here.

One further general trend that seemed clear (though we did not collect standardized observations) was that in all the *Latrodectus* and *Steatoda* species, younger spiders built relatively complete webs more quickly, often during a single night, while adults added lines more slowly, over many nights. This might appear to be an exception to the ontogeny repeats phylogeny pattern, because gradual accumulation of lines is surely an ancient trait in spiders in general (Eberhard 1990). But if theridiids are descended from an orb-weaving ancestor (Agnarsson 2004; Arnedo et al. 2004), in which the entire web was presumably built in one burst of construction, then the gradual addition of lines by adult theridiids may be a secondarily derived trait.

Our observations of *Steatoda* differ in at least one respect from those of Benjamin & Zschokke (2002) on *S. triangulosa*. There were no radially arranged lines centered on the retreat at the edge of the web, as described by Benjamin & Zschokke (2002).They also stated that cut and reel behavior did not occur in *S. triangulosa*, while we found that in both *Steatoda* species at least some gumfoot lines clearly had a small white mass of fluff near the site where the gumfoot line was attached at its upper end. These masses suggest that the spider cut and then reeled up the line as it moved upward during gumfoot line construction (Eberhard et al. 2008a). Many gumfoot lines in the webs of both *S.* nr. *hespera* and *S. grossa* appeared to lack these white specks, however, and direct observation (with good viewing conditions) of the construction of one gumfoot line by an adult female of *S.* nr. *hespera* clearly showed a lack of cut and reel behavior. Thus cut and reel is not necessarily a part of all gumfoot line construction in *Steatoda*.

We cannot evaluate the possibility that gumfoot line construction in *Latrodectus* also occasionally occurs without cut and reel behavior. We observed some gumfoot lines lacking a mass of fluff at the upper end. However, if the cut line tangled on other web lines while it was still more or less extended and thus before it collapsed on itself in a single mass, the white speck would be reduced or eliminated. In addition, we did not successfully locate the upper ends of all gumfoot lines, perhaps because the upper end was sometimes in the middle of the tangle, so some white specks there could possibly have been missed. Thus we cannot be sure that all failures to find fluff masses were due to a lack of cut and reel behavior.

Ontogenetic changes in abdomen coloration from lighter to darker colors are apparently widespread in *Latrodectus* (Kaston 1970). Our field observations of *L. mirabilis* suggest that the ontogenetic change in abdomen color in this species is associated with changes in its web design. Younger-instar spiders had light-colored abdomens (mostly white in at least the three first instars), built webs at exposed sites and rested in the central portion of these webs. The light color of a spider with few or no prey remains would probably reduce its visibility; at the site where we observed them, the predominant abdomen color was similar to that of nearby rocks. Older-instar nymphs and adult females had much darker abdomens (black, with fine yellow and red markings), and their webs generally had a retreat at the edge, where the spider rested in the dark under an overhanging rock. The ontogenetic change in retreats involved both the site of the retreat (in the open vs. under a rock) and the placement of prey (often substantial numbers attached in a tight mass to the retreat vs. lower numbers scattered near or below the spider's resting place and not directly above it). A similar change in abdomen color from light to dark occurs in both *L. geometricus* and *L. hesperus* (?), and free-ranging young spiders of both species also rested

exposed in the midst of their webs during the day, while older nymphs and adults of *L. geometricus* rested in retreats at or beyond the edge of the web during the day. Further observations of immature spiders in nature will be necessary to determine whether, as predicted by our idea, younger individuals of other *Latrodectus* species with light-colored juveniles generally rest at more exposed sites during the day than older, darker individuals.

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A new species of *Tarabulida* (Solifugae: Daesiidae) from Kenya, with the first complete description of a male of the genus

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Abstract. We describe a new species of *Tarabulida* Roewer 1933 from Kenya. This genus was previously known from only two species (*Tarabulida ephippiata* Roewer 1933 and *Tarabulida fumigata* Roewer 1933) from Libya, which were described from specimens reported as females. *Tarabulida mugambii* new species is based on specimens collected in northwestern Kenya, representing the first complete description of a male *Tarabulida* and the first record for the genus from Kenya. We also discuss problems associated with characterizing *Tarabulida* and its placement within the Daesiidae. A lectotype is designated for the type species of *Tarabulida*, *T. ephippiata* Roewer 1933.

Keywords: Solifuges, camel spiders, *Blossia*

The diversity of solifuges in Kenya is poorly known; there are only 36 species recorded from this country (Harvey 2003) and seven formally described subspecies. Roewer's monograph (1932–34) provides the only comprehensive insight into solifuges of Africa and while the revisions by Lawrence (1955, 1960, 1962, 1963, 1968, 1972) are excellent, they mainly focus on the solifuges of southern Africa. Roewer provided continuous updates to his monographic treatment through 1961 with several of these works including solifuges from northern and central Africa (Roewer 1941, 1951, 1952a, 1952b, 1954, 1961). Subsequent to Roewer, very limited work has been completed on solifuges from northern and central Africa. This work is not at all comprehensive and generally focuses on a limited number of species (Panouse 1955, 1957, 1960a, 1960b, 1964; Kraus 1959; Junqua 1962, 1963, 1966; Levy & Shulov 1964; Panouse et al. 1967; Della Cave & Simonetta 1971; Thaler 1982; Gromov 1998, 2000).

This paper focuses on the small and little known genus *Tarabulida* Roewer 1933 in the family Daesiidae. Roewer (1933) described *Tarabulida* from three female specimens, representing two species. Roewer (1933) placed *Tarabulida* in his newly created subfamily Gnosippinae, the latter defined by the 1-1-1-1 tarsal formula shared by *Tarabulida* and the four other originally included genera. The type species of *Tarabulida*, *T. ephippiata* Roewer 1933, was described from Tripoli in Libya. The second species, *T. fumigata* Roewer 1933, was described from Cyrenaica, a large region in eastern Libya bordering Egypt. Males of these species are unknown, but Maury (1980) partially described the flagellum of a "*Tarabulida* sp." while making comparisons between several Old World daesiids and two South American species that he included as the first New World members of the Daesiidae. Although Maury (1980) did not indicate the provenance of this specimen, or who made the determination, he acknowledged curators at the American Museum of Natural History (AMNH) and the Museum of Comparative Zoology (MCZ) for providing specimens for comparison. We describe a new species of *Tarabulida* from Kenya based on an adult male specimen, an adult female specimen and several immatures, provide comparisons with previously described species, and comment on the placement of *Tarabulida* within Daesiidae.

METHODS

The terminology for leg spination formulae and pedipalp spination follows Roewer (1933). The term 'ctenidia' is also used as in Roewer (1933). Dentition descriptions largely follow Roewer (1933); however, we utilize a more detailed description of teeth in line with Pocock (1895). The terms 'median' and 'lateral fondal,' or cheek teeth follows Muma (1951) and Wharton (1981). Images were acquired digitally using Syncroscopy's Auto-Montage Pro 5.01.0005 (Copyright Synoptics Ltd.) and PictureFrame (TM) Application 2.3, in combination with a ProgRes 3008 digital camera mounted on a Leica MZ APO dissecting microscope.

The specimens of *Tarabulida* described below were examined as part of a larger survey targeting the diversity and distribution of solifuges in Kenya. The holotype and three immature specimens were collected from Lokichoggio Township, located approximately 30 km from the Sudan border in northwestern Kenya. They were collected from under rocks in shallow depressions in a dry riverbed and at the base of the Mogilla Range, (04.210180°N, 34.375030°E), a fault accumulation made up predominantly of trachyte, rhyolite and associated tuffs (Champion 1937). A female specimen collected a little further east at 'Lake Rudolf' (= Lake Turkana) was discovered amongst unsorted material in the National Museums of Kenya (NMK). The holotype and paratypes of the newly described species from Kenya were stored in 80% ethanol and will be deposited in NMK. The left chelicera of the holotype was used for DNA analysis as part of a larger study. Additional material examined included the syntypes of *T. ephippiata* and holotype of *T. fumigata* (all three specimens from Senckenberg Forschungsinstitut und Naturmuseum) and a male and female specimen from the American

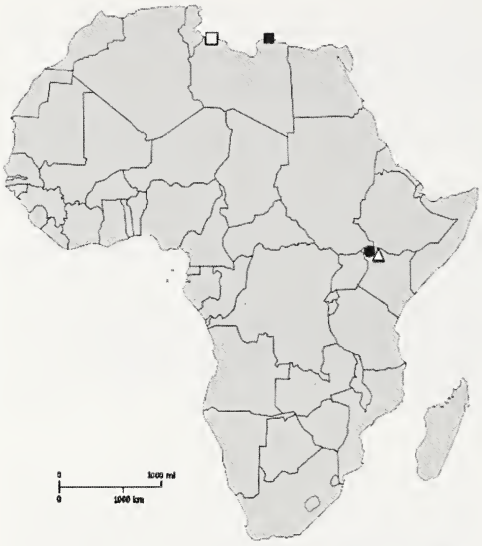


Figure 1.—Distribution of the genus *Tarabulida* in Africa. White square, *T. ephippiata* type locality. Black square, *T. fumigata* probable type locality. Black circle, *T. mugambii* locality for holotype and immature paratypes. White triangle, *T. mugambii* female paratype locality.

Museum of Natural History, New York (AMNH) determined as *Tarabulida* by Bruno Lamoral. Localities of *T. ephippiata* and *T. fumigata* depicted in Fig. 1 were taken from Roewer (1933).

TAXONOMY

Family Daesiidae Kraepelin 1899
Genus *Tarabulida* Roewer 1933

Type species.—*Tarabulida ephippiata* Roewer 1933 by original designation.

Remarks.—*Tarabulida* was described by Roewer on the basis of two species represented by three specimens that shared the following characters: 1.2.2.2 chaetotaxy on tarsi of legs II and III, 2.2.2.2.2 chaetotaxy on tarsi of leg IV and 5 dorsal spines on the metatarsus of legs II and III. Problems associated with this characterization are treated in the discussion section following the description of *Tarabulida mugambii*.

Tarabulida mugambii new species
(Figs. 2–9)

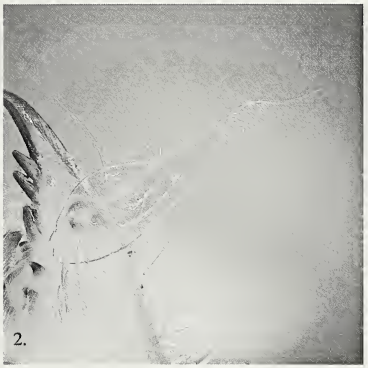
Material Examined.—Holotype adult male: KENYA: *Rift Valley Province*: Lokichoggio, base of Mogilla Range, 04.210180°N, 34.375030°E, 18 March 2007, Reddick, Wharton and Mugambi (NMK). Paratypes: KENYA: *Rift Valley Province*: 1 adult female, Op. Drake Station, Lake Rudolf, 03.53333°N, 36.2°E, 8 August 1980 (NMK); 1 immature, Lokichoggio, base of Mogilla Range, 04.210220°N, 34.376780°E, 18 March 2007, Reddick, Wharton and Mugambi (NMK); 1 immature, same locality, 04.210330°N, 34.375510°E, 16 March 2007, Reddick, Wharton and Mugambi (NMK); 1 immature, Lokichoggio, NW of town, near military barricade, 04.213020°N, 34.350620°E, 17 March 2007, Reddick, Wharton and Mugambi (NMK).

Etymology.—This species is named after Mr. Joseph Mugambi, a lead research assistant from the National Museums of Kenya.

Diagnosis.—*Tarabulida mugambii* is most readily differentiated from the two previously described species of *Tarabulida* by the presence of spines and cylindrical bristles on the pedipalps. In the other two species, the pedipalps lack spines and cylindrical bristles. The coloration of *T. mugambii* also differs greatly from the two other described species of *Tarabulida*, though this is based primarily on the original descriptions since the syntypes of *T. ephippiata* and holotype of *T. fumigata* (Fig. 10) are badly faded for the most part. From the original description, the opisthosoma of *T. ephippiata* has black pleura separated by a broad band of yellow tergites, with tergites 8–10 also black. The opisthosoma of *T. mugambii* is uniformly medium brown, including tergites, sternites, and pleura; *T. mugambii* is thus somewhat darker than the similarly uniformly colored *T. fumigata*. The malleoli of *T. ephippiata* are edged with black, whereas *T. mugambii* and *T. fumigata* have completely white malleoli. The chelicerae and propeltidium are entirely black in *T. fumigata* but light golden-brown in *T. mugambii* and darker brown in *T. ephippiata*. *Tarabulida mugambii* lacks the black bands associated with legs III and IV of *T. fumigata*, and has a different color pattern on the pedipalps than in the other two species: broadly dark medially, pale basally and apically vs. multiple bands of dark and pale in the previously described species. Of less importance, all three species bear dorsal spines on the metatarsus of Legs II and III; however, in *T. ephippiata* and *T. fumigata*, these spines are much thicker and shorter than in *T. mugambii*. The opisthosomal pleura are also evenly, densely setose in *T. ephippiata*, while in *T. fumigata* and *T. mugambii* the pleura are more sparsely setose.

Description.—*Adult male:* Coloration (based on ethanol-preserved specimens): Legs, propeltidium, and chelicerae entirely light golden-brown. All joints on all legs slightly darkening to purple-brown near each articulation. Anterior margin of propeltidium outlined with very thin dark brown line extending posteriorly to delineate exterior lobe of prosoma from rest of propeltidium. Femur and tibia of pedipalps light brown but slightly darker, almost purple-brown, towards distal end of tibia. Coxa, trochanter, metatarsus, and tarsus of pedipalp entirely white. Opisthosoma entirely medium brown (darker than golden-brown of legs) with wide terga (Fig. 8) the same color. Arcus posterior, meso- and metapeltidium medium brown with integument between same color as legs. Malleoli entirely white. Alcohol-preserved material somewhat leached relative to living specimens with legs, propeltidium, and chelicerae more reddish and purple-brown areas darker, with a richer color.

Flagellum: Paraxially moveable, membranous, broad basally, gradually tapering distally, margins slightly in-curled at base (Fig. 2). Ventral and dorsal margins of tapered, distal half with projections resembling cilia on leaves of a Venus Fly-Trap plant. Flagellum apically slightly bent and spiraling at


2.


3.


4.


5.

Figures 2–5.—*Tarabulida mugambii* new species: 2. Flagellum; 3. Dentition of male holotype with lines pointing to principal setae; 4. Paired spines on pedipalp of male holotype; 5, Dentition of female paratype.

distal end of in-curled margin (Fig. 2). Apex of flagellum very thin and hair-like with no projections.

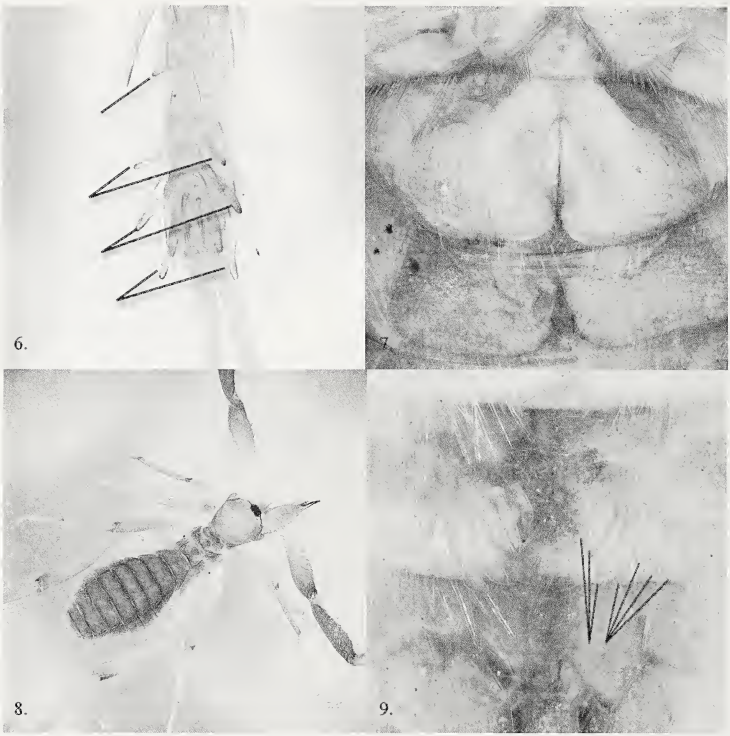
Dentition: Moveable finger with two large triangular teeth and a smaller median tooth, situated closer to the proximal large tooth than the distal one (Fig. 3). Four small lateral fondal teeth approximately subequal in size. Two larger median fondal teeth concealed behind mesal surface cheliceral bristles, with the one closest to base of rostrum having a distinct, deep notch. Immoveable finger comprised of three teeth. Two distal teeth long, thin, narrowly triangular, strongly slanted toward apex of chelicerae. Third tooth large, more broadly triangular, with very small triangular dorsal notch, resembling an extra small tooth.

Legs: Leg I with no claws. Legs II–IV with 2 long hairless claws. All legs covered uniformly with short thin hairs. Dorsal surface of metatarsi 2 and 3 with a row of 5 long spines. Tarsal segmentation 1-1-1-1. Tarsi of fourth leg partially divided by weakly indented line, the two divisions not articulated. Ventral spination on tarsi 2 and 3 is 1.2.2.2 (Fig. 6). Ventral spination on tarsi 4 is 2.2.2.2.2.

Chaetotaxy: Chelicerae with many thick spines, ranging in size from very small to long, longer spines forming a line dorsomedially along chelicerae. Two long, slender, apically directed principal setae present dorsally on immoveable finger, adjacent flagellum (Fig. 2). Propeltidium covered in spines of varying length, most notably, lined with spines along posterior edge, some pointing anteriorly, some posteriorly, giving appearance of a collar. Posterior margins of plagula mediana tergite, mesopeltidium, and metapeltidium also with rows of thick spines. Opisthosoma segments II–VII with dorso-lateral clusters of spines, spines gradually decreasing in thickness posteriorly. Pleura sparsely setose. Ventral surface of both femur and tibia of pedipalp lined with long spines interspersed with shorter cylindrical bristles, arranged primarily in two distinct rows. Metatarsus of pedipalp with six pairs of shorter, evenly spaced spines of equal length (Fig. 4). Body otherwise sparsely setose throughout.

Ctenidia: First postgenital sternite with a group of seven long, broad, pointed ctenidia on each side of midline (Fig. 9), golden brown in color.

Adult female: Coloration (based on ethanol-preserved specimen): as in male except coloration of the tergites lighter due to leaching in alcohol. Legs of female not darkening to the same degree as male on leg joints, but there is evidence of some darkening.



Figures 6–9.—*Tarabulida mugambii* new species: 6. Leg III tarsal spines showing the 1.2.2.2 pattern indicative of *Tarabulida* spp.; 7. Genital plate of female paratype; 8. Dorsal habitus of male holotype; 9. Ctenidia on male holotype with lines pointing to ctenidia on right side.

Dentition: Moveable finger with two large well-worn teeth with a smaller median tooth, situated closer to the proximal tooth than the distal one (Fig. 5); median tooth much closer to proximal tooth than in male (Fig. 3). Cheek teeth as in male. Cheliceral bristles as in the male but much thicker and more numerous. Immovable finger with four medium-sized teeth, the most proximal 2 very close together to give the impression of being almost joined. Teeth of female more rounded than in male and not pointing distally as in male. Dorsal surface of immovable finger with small elevation proximal to fang tip, that gives the impression of a dent or pit on the dorsal surface of the chelicera.

Legs: as in male, however dorsal spines on legs II and III thicker than on male.

Chaetotaxy: As in male, except female lacks the two long, slender, apically directed principal setae present dorsally on immoveable finger of chelicerae (Fig. 5).

Ctenidia: No fully formed ctenidia; however, there are slightly thickened hairs on the post-genital plate.

Genital sternite: Modified, clearly bilobed with deep median indentation and posterior margin free (Fig. 7).

Immatures: Coloration (based on ethanol-preserved specimens): as in male in two larger immatures, however the smallest immature is almost devoid of color.

Dentition: Dentition of immatures similar to male, except notched cheek tooth of holotype represented as two separate teeth in immatures. Thus, immatures with three separate median fondal teeth and four separate teeth on immoveable finger. Distal teeth on immoveable finger of immatures vertical, not slanted distally.

Legs: As in male, but thicker and shorter in the largest specimen relative to the two smaller specimens; dorsal spines poorly developed or nonexistent in smaller immatures. Smallest specimen with 3 claws on Legs II–IV indicating a very early instar.

Chaetotaxy: As in male, including pedipalp spination, however all spines present on immatures much weaker than in adults. Immatures lack the principal setae on the immoveable finger of chelicerae.

Ctenidia: No ctenidia present on immatures.

Dimensions: Male holotype: Total body length including chelicerae, 16 mm; length of chelicerae, 3 mm; length of leg IV,

20 mm; length of pedipalp, 15.5 mm. Female paratype: Total body length including chelicerae, 21 mm; length of chelicerae, 4.5 mm; length of leg IV, 16.5 mm; length of pedipalp, 14 mm. Immature paratype 1: Total body length including chelicerae, 5 mm; length of chelicerae, 1 mm; length of leg IV, 4.5 mm; length of pedipalp, 3.5 mm. Immature paratype 2: Total body length including chelicerae, 10 mm; length of chelicerae, 2 mm; length of leg IV, 8 mm; length of pedipalp, 7 mm. Immature paratype 3: Total body length including chelicerae, 10 mm; length of chelicerae, 3 mm; length of leg IV, 14 mm; length of pedipalp, 10 mm.

Distribution.—The distribution of the genus *Tarabulida* is shown in Fig. 1. The square icons indicate the type localities for *T. ephippiata* and *T. fumigata*. Libya: Tripoli Province, Tripoli (formerly Tarabulus) (*T. ephippiata*); Cyrene (formerly Kyrenaika) (*T. fumigata*). The triangular icon indicates the type locality for *T. mugambii*. Although the data label for *T. fumigata* indicates only Kyrenaika, a very large region bordering Egypt in present-day Libya, the specimen is likely to have been collected in the coastal area of this region since the place name 'Kyrenaika' is also known as Cyrenaica or the city of Cyrene in what is now Shahhat, Libya. Also, at the time of Roewer's original descriptions travel into the interior of Libya would have been less likely, as road infrastructure would have been restricted to the coast.

The distribution gap between *T. mugambii* and the two previously described species is considerable (Fig. 1), but the geographic isolation of *T. mugambii* from the other species in the genus can be readily explained by the virtual absence of collections and described species from intermediate areas (Harvey 2003). We therefore predict a more or less continuous distribution for *Tarabulida* for this area wherever suitable habitats exist. The inadequate and patchy collection history has been used to explain large gaps in distribution and low diversity in other areas of Africa as well (Lamoral 1973).

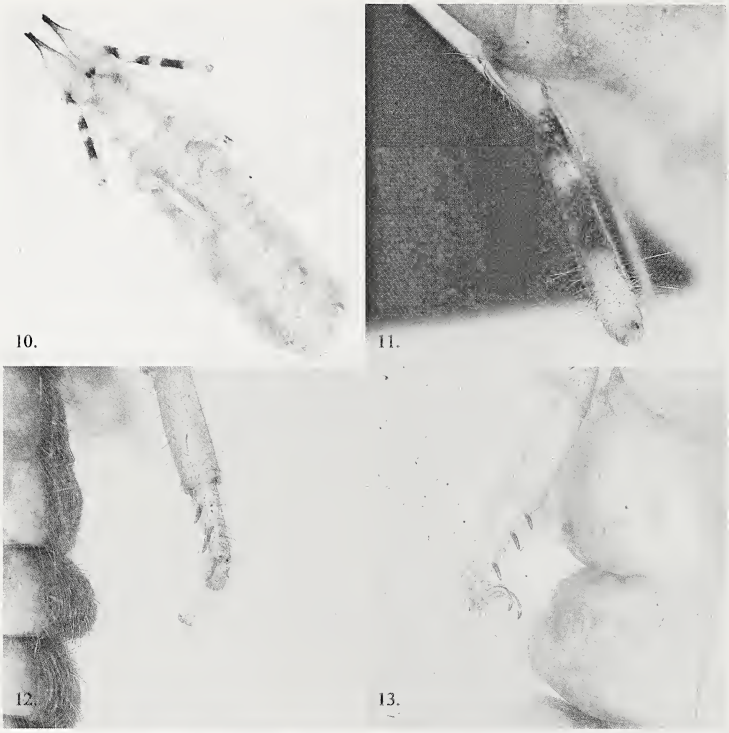
Ecology.—We collected the male and immature specimens of *T. mugambii* from under rocks during the day, which indicates nocturnal activity. The habitat was extremely hot and dry but subject to periodic flooding from the nearby seasonally dry river bed, and solifuges were found in shallow depressions under rocks along the base of a large hill. The hills and river bed were sparsely populated with small bushes and various xeric plants. The vegetation of the area where they were collected is categorized as Somalia-Masai desert grassland and shrubland (White 1983), with a rainfall of 100–200 mm per year.

DISCUSSION

Tarabulida mugambii is unquestionably a member of the family Daesiidae, based on the absence of claws on leg I, the presence of a paraxially moveable, malleable, membraneous flagellum, and the 1-1-1-1 tarsal formula. Within the Daesiidae, the male holotype and associated paratypes fit the description of Gnosippinae and *Tarabulida* put forth by Roewer (1933) based on the 1-1-1-1 tarsal formula and the 1.2.2.2 tarsal spination on legs II and III (Fig. 6). This particular arrangement of tarsal spines is very different from all other genera in the subfamily Gnosippinae and thus, within the context of Roewer's classification, the specimens described here clearly belong in *Tarabulida*. Roewer's (1933) classification of Daesiidae, and for that matter, all of the Solifugae, which relies almost exclusively on tarsal formulae and chaetotaxy, has been severely criticized (Lawrence 1955, 1963; Simonetta & Delle Cave 1968; Della Cave & Simonetta 1971; Wharton 1981). We therefore provide an extended discussion of our rationale for including this new species in *Tarabulida* along with an associated commentary on the larger issue of the generic classification of daesiids.

In direct contrast with *T. mugambii*, the two specimens on which Roewer (1933) based his description of *Tarabulida* lack both ctenidia on the postgenital sternites and thickened spines on the pedipalps (Fig. 11). The presence or absence of ctenidia and the pattern of spination on the pedipalps are useful for discriminating among species in other daesiid genera, such as *Blossia* Simon 1880 and *Hemiblossia* Kraepelin 1899 (Wharton 1981), but the ctenidia in particular may also vary intraspecifically associated with age-related development and/or sexual dimorphism (Wharton 1981; Brookhart & Cushing 2005). In *T. mugambii*, ctenidia are distinctly broadened, fleshy structures in the adult male, but absent in all of the immatures, representing three size classes. The adult female has slightly thickened hairs on the post-genital sternite, not obviously different from those on the more poorly preserved specimens of *T. fumigata* and *T. ephippiata*. The absence of ctenidia in *T. fumigata* and *T. ephippiata*, known only from females (Roewer 1933) and an immature (our assessment of type material), is thus of little assistance either in discriminating among these three species or in clarifying their generic affinities. Similarly, pedipalp spination has been reported to vary intraspecifically in daesiids, as exemplified by sexual dimorphism in *Gnosippus klunzingeri* Karsch 1880 recorded by Roewer (1933), though this requires verification. More commonly, however, variation in pedipalp spination pattern is a useful diagnostic tool for separating species among the Daesiidae. *Hemiblossia brunnea* Lawrence 1953, for example, has a bottle brush-like pattern of spines and setae around the entire circumference of the pedipalp metatarsus and tarsus, whereas *H. australis* Purcell 1902 possesses only paired spines on the ventral sides of the pedipalps from the tarsi to the tibia (Roewer 1933). Wharton (1981) provided similar examples for *Blossia*. In *T. mugambii*, the pedipalp spination pattern of the adult male holotype and the adult female is also found in all immature specimens, suggesting that it will be a useful diagnostic character for this species relative to *T. fumigata* and *T. ephippiata*. As with the ctenidia, however, the value of pedipalp spination pattern for generic-level diagnoses remains dubious and thus sheds no light on the placement of *mugambii* within the Daesiidae.

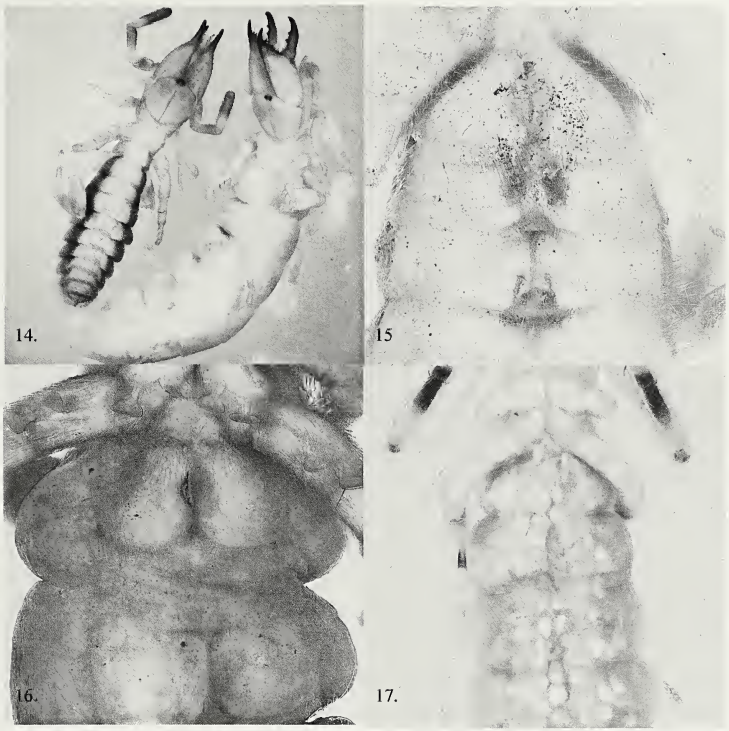
Placement of our newly described species in *Tarabulida* is a necessary outcome of its inclusion in Roewer's Gnosippinae based on the 1-1-1-1 tarsal formula. Yet Roewer's subfamily classification for Daesiidae has been justifiably criticized because it was established solely on differences in numbers of tarsal segments on legs II, III, and IV (Roewer 1933). Hewitt (1919), Della Cave & Simonetta (1971), Lawrence (1972), and Wharton (1981), working primarily with different species, have all documented variation in tarsal segmentation between the left and right legs of various individuals, noting that this phenomenon is sufficiently commonplace to render proposed classifications ineffectual. Thus, at least some genera, such as *Broomiella* Pocock 1902, have been based on



Figures 10–13.—*Tarabulida* type specimens: 10. Dorsal habitus, *T. fumigata* holotype; 11. Pedipalp setation, *T. fumigata* holotype; 12. Dorsal spines of metatarsus leg III, *T. ephippiata* lectotype; 13. Dorsal spines of metatarsus leg III, *T. ephippiata* paralectotype.

individuals with tarsal anomalies (Hewitt 1919; Lawrence 1972), while similar anomalies have led to the assignment of apparently related species to different genera in different subfamilies (see especially Della Cave & Simonetta 1971). With this in mind, it is useful to consider genera outside Roewer's Gnosippinae for the placement of *mugambii*, and *Blossia* is a logical choice. Roewer (1933) used the pattern of ventral spines on the tarsi to define genera within each subfamily and described identical patterns for *Tarabulida* of the Gnosippinae and *Blossiola* Roewer 1933 of the Blossiinae. Wharton (1981) treated *Blossiola* as a synonym of *Blossia*.

In *T. mugambii*, the shape of the flagellum and ctenidia, the presence of principal setae, and the pattern of the cheliceral dentition in the holotype are all consistent with a placement in *Blossia*. The flagellum, though distinctive (Figs. 2, 3), nevertheless shares basic structural similarities with those of species such as *Blossia setifera* Pocock 1900 and *Blossia massaica* Roewer 1933. Unfortunately, these flagellar, ctenidial, setal, and dentition characteristics are all male-specific, and Roewer (1933) did not have any males when he described *Tarabulida*. Thus, the only obvious difference between *Tarabulida* and *Blossia*, based on Roewer (1933), is the number of tarsal segments on leg IV. We have therefore somewhat reluctantly placed the new species in *Tarabulida* because there is only one tarsal segment on leg IV. Even this characterization is unsatisfactory, however, because in the *T. mugambii* holotype and the associated female, leg IV has a weak suture line extending halfway around the tarsus at its midpoint (though there is no evidence of articulation between the two halves). The suture line on the female is admittedly much weaker than that on the male, and the two larger immatures similarly have a partial suture line, though also not as well developed as on the male. The type specimens of *T. fumigata* and *T. ephippiata* have the leg IV tarsus clearly one-segmented with no trace of a partial suture. The only other difference between *Tarabulida* and *Blossia* that can be extracted from Roewer's (1933) descriptions is the number of dorsal spines on the metatarsus of legs II and III (3 in *Blossia*, 5 in *Tarabulida*, according to Roewer 1933). Unfortunately, examination of the type specimens of *T. ephippiata* and *T. fumigata* reveals that the dorsal spination on the metatarsus (Figs. 12, 13) is variable in both species, with 3 dorsal spines on some legs and 5 on others. In both the male and female specimens of *T. mugambii*, there are 3 distinct dorsal spines and occasionally one or two



Figures 14–17.—*Tarabulida* type specimens: 14. Size difference between types of *T. ephippiata*; 15. Genital sternite of *T. ephippiata* lectotype; 16. Genital sternite of *T. ephippiata* paralectotype; 17. Genital sternite of *T. fumigata* holotype.

weaker ones. The spines on our specimens are thus consistent in number and placement with Roewer's type material. Roewer's (1933) description unfortunately does not encompass the variation we observed among the specimens he had before him when he described *Tarabulida*. A further problem is that the spines are difficult to count because Roewer (1933) referred to all of the spines as dorsal, but two of these are more latero-anteriorly displaced. These latter two are sometimes poorly developed and thus not spinose in appearance.

In general appearance, *T. ephippiata*, and especially *T. fumigata*, resemble the species of *Hemiblossia*, while *T. mugambii* more closely resembles many of the species of *Blossia*. This is due to the fact that the appendages, including the pedipalps, are shorter in *T. fumigata* and *T. ephippiata*, with tarsi and metatarsi shorter and deeper relative to the longer, more slender tarsi and metatarsi of *T. mugambii*. Although male solifuges often have longer legs (and therefore longer leg segments) than females, making such comparisons challenging, both males and females of *Hemiblossia* have relatively short legs and pedipalps. The absence of males of *T. ephippiata* and *T. fumigata* precludes a more meaningful assessment based on appendage size. The comparison of *T. fumigata* (Figs. 10, 11) and *T. ephippiata* (Fig. 14) with *Hemiblossia* is enhanced by the dark color patterns recorded by Roewer (1933) in his original descriptions of these two species, particularly the black pleura of *T. ephippiata* and the black chelicerae and propeltidium of *T. fumigata*. Unfortunately, the larger and more clearly female syntype of *T. ephippiata* is now completely pale, and the second syntype, though retaining the dark pleura and some banding on the appendages, is also badly leached with the prosoma, described as brown in the original description, now dull yellow. The holotype of *T. fumigata* is also badly leached and there is no longer any trace of black on the chelicerae.

The two syntypes of *T. ephippiata* are dissimilar in appearance (Fig. 14) and have structural differences (e.g., genital and postgenital sternites, Figs. 15, 16) that suggest the possibility that these may not be conspecific. Since this is the type species of *Tarabulida*, a lectotype designation therefore seems appropriate and we hereby designate the smaller of the two specimens (specimen on the left in Fig. 14) as the lectotype. The other specimen becomes a paralectotype. Both specimens are apparently adult females, as suggested by the modified genital sternites. Another difference between the two specimens of *T. ephippiata* is the pedipalp spination. The smaller of the two has more densely bristled metatarsi and

tarsi than does the larger. The holotype of *T. fumigata* (Fig. 10), which has the prosoma much more *Hemiblossia*-like, appears to be an immature specimen, with no modifications of the genital sternite and no apparent opening (Fig. 17).

We also examined two specimens from AMNH, collected in Morocco and determined as *Tarabulida* by Bruno Lamoral. There is one male and one female in a single vial, and we suspect the male is the specimen partially described by Maury (1980). The dark body and the spination pattern on legs II and III, both ventrally and dorsally, fit Roewer's description of *Tarabulida*. However, the tarsi of leg IV are clearly divided into two segments, and the flagellum is characteristic of that found in *Gluviopsis* Kraepelin 1899 (though neither the segmentation nor spination pattern of leg IV match that of *Gluviopsis*). As with *T. mugambii*, these specimens are similarly difficult to place because the color pattern and relatively short leg segments match *Tarabulida*, the leg segmentation matches *Blossia* and the spination pattern fits both.

We conclude, as have others have (noted above), that Roewer's subfamily classification of Daesiidae gives a misleading impression of relatedness among the genera and hinders correct application of generic names to newly discovered species. A detailed revision of the species groups of *Blossia* and *Hemiblossia*, possibly along the lines suggested by Hewitt (1919) and Wharton (1981), is essential for an improved understanding of the placement of *Tarabulida* within Daesiidae, including assessment of whether or not it can be retained as a valid taxon. However, it will be difficult to undertake a meaningful revision of *Hemiblossia* without a better sampling of correctly associated adult males and females. Similarly, in order to fully characterize *Tarabulida*, it will be essential to collect males of *T. ephippiata*, the type species, and *T. fumigata* since secondary sexual characteristics are important for delineating species groups within Daesiidae. Knowledge of flagellar morphology in particular will assist in assessment of relationships among *Tarabulida*, *Blossia*, and *Hemiblossia* and thus considerably facilitate future placement of species such as *T. mugambii*.

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Courtship, mating, and cocoon maintenance of *Tricca lutetiana* (Araneae: Lycosidae)

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Abstract. *Tricca lutetiana* (Simon 1876) (Lycosidae) lives hidden underground and, thus, is not well known. Our objective was to document more fully basic information on reproduction, particularly copulation, in this species. We obtained and observed in the laboratory 86 individuals from the wild between 2006 and 2008. Vibratory and tactile communication is an important medium during sexual communication. We described unique movements of the mating male's legs during copulation, for the first time in the family Lycosidae. Adult females live for two years and, in their underground burrows, they produce one cocoon per season. They carry the cocoon, mostly using legs IV, and look after it for one month until the offspring leave. Maternal care for spiderlings lasts one week following the spiderlings' emergence.

Keywords: Wolf spider, life history, copulation, tactile communication, Czech Republic

Wolf spiders are famous for their courtship behavior (e.g., Bristowe & Locket 1926; Kaston 1936; Kronestedt 1990; Töpfer-Hofmann et al. 2000; Stratton 2005, and references therein). However, few papers have been published with the sole purpose of describing copulation patterns of certain spider species (e.g., Rovner 1971, 1973; Costa & Sotelo 1994), on cocoon making, and on parental care for cocoons and offspring (e.g., Vlijm 1962; Eason 1964). Montgomery (1903) described life histories of ten lycosid species very precisely, and Engelhardt (1964) described those of four *Trochosa* C.L. Koch 1848 species. Stratton et al. (1996) summarized data on copulation patterns. All those authors focused on common species; however, behavior of rare species has remained unknown.

Tricca lutetiana (Simon 1876) is a European (including Ural), extra-Mediterranean wolf spider (Buchar & Růžička 2002). It ranges from France (Le Peru 2006) in the west to the European central part of Russia (Esjunin et al. 1993) in the east, and from the southernmost part of Scandinavia (Almquist 2005) in the north to Bulgaria (Blagoev 2007) in the south. It has not been found on the British Isles and Pyrenean Peninsula. The species inhabits forest steppes, warm blackthorn shrubs, sun-exposed forest margins, and rock steppes (Buchar & Růžička 2002). Before the use of pitfall trapping in the 1950s, researchers were only familiar with a few specimens from collections (Buchar & Thaler 1995). Therefore, the species was believed to be rare (Wiebes 1956; Braun 1963).

The biology of the species is still almost unknown. Koch (1878) noted that the cocoon of the species is round, white, and reaches five mm in diameter. Wiebes (1956) captured 75 males in May and June using pitfall traps and identified that period as the time of copulation, despite capturing no females. Dolejš (2006) obtained data similar to Wiebes and described the males as nocturnal, active mainly between 03:00–06:00 h under laboratory conditions and compatible with one another in captivity. No exact data on population density are available, but the density seems to be very high on forest/rock steppes, as males of the species are the most abundant specimens in pitfall traps after a rainy night or in dew (J. Buchar & P. Dolejš pers. obs.).

Wiebes (1956) hypothesized that females may be found conducting yet unobserved sedentary life habits. Dolejš et al. (2008) described burrows of and prey capture by females and juveniles. The burrows are entirely underground, mostly globular and enclosed, with no entrance and no exit leading to the surface. They are situated either under a stone or under the surface without vegetation, reaching at most three cm deep. The burrows are not silk-lined, and spiders prey inside them using the "sit-and-wait strategy." Such a construction of a burrow is unique to this species. Neither juveniles nor females venture out to feed in epigeon (= ground layer: soil surface, spaces under stones, litter, moss and lichen layer, lower herb stems up to five cm). The species hunts small soil animals that enter spiders' burrows when moving through the ground (Dolejš et al. 2008). Probable prey include Enchytraeidae (P. Dolejš pers. obs.), Collembola (Sanders & Platner 2007) and small insect larvae (Dolejš 2006). All these organisms are very abundant in the spiders' locality (P. Dolejš pers. obs.). To date, nobody has studied the phylogeny of this species because it is difficult to find living study animals, as they live hidden in the soil.

Here we followed the appeal by Stratton et al. (1996) to examine more species of lycosids for patterns of copulatory behavior. We focused on *T. lutetiana*, a hidden species that has never been studied before. Our aims were to describe courtship, copulation, and maternal care of the species.

METHODS

We used the methods described in Dolejš et al. (2008) to collect living males, females, and juveniles. The study took place in two National Nature Reserves – NNRs (Dřínová hora in Karlštejn NNR: elev. 345 m, 14°09′39″E, 49°56′30″N, and Koda NNR: elev. 350 m, 14°07′18″E, 49°56′04″N) in Český kras (Bohemian Karst) Protected Landscape Area in the Czech Republic. The Government of the Czech Republic permitted the research in NNRs by the decree no. 1159/07. In this study we used 39 males (eight of them were reared from juveniles) and 47 females (16 of them were reared from juveniles). Voucher specimens (P6A-4926) are deposited in the National Museum (Cirkusová 1740, CZ – 193 00 Praha 9 – Horní Počernice, Czech Republic).

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We studied aspects of the biology of *T. lutetiana* in a laboratory. To imitate adult females' natural conditions and to provide them an opportunity to make burrows, we kept them in glass terraria as described in Dolejš et al. (2008). As the species does not seem to be territorial (we even found three females under one stone in the field), we placed up to two females in one terrarium; nevertheless, we divided the terrarium diagonally in such cases. We held juveniles and males in plastic test tubes (length 10 cm, diameter 15 mm) with wet cotton wool as a source of water. When the juveniles matured into females, we housed them in the terraria as described above. Rearing temperature (day/night: winter = 5/5° C, summer = 26/20° C) followed temperature at the collection sites. We set the photoperiod every week according to the actual sunrise and sunset (winter solstice: 8L:16D, summer solstice: vice versa).

We observed and videotaped (digital Olympus C-7070 WZ camera and Panasonic NV-GS400 video camera) the courtship and mating of focal individuals placed in Petri dishes (diameter 5 cm, depth 14 mm) or directly in the terrarium, where the females lived, at room temperature (21–26° C). To examine substratum and burrow effects on courtship and mating behavior, we conducted the trials in terraria; to describe details that were not observable in terraria, we conducted the trials in Petri dishes. We tested all available adult females with randomly chosen males. Out of 100 trials recorded, we observed and analyzed 37 copulations (29 in Petri dishes and eight in terraria). As our aim was to describe copulation and maternal care, we tested all available females until they mated or produced cocoons. Therefore, we tested nineteen females once and the rest of females multiply. Twelve males (out of 39) copulated once and the rest of males copulated multiply. In total, 32 females (out of 47) mated.

We placed a piece of white, moistened filter paper into the Petri dish to provide a substrate suitable for spiders' locomotion, to improve contrast during videotaping, to allow the spiders to remain hydrated, and to prevent the females from hiding under the paper (females had a tendency to hide under dry filter paper). We placed an adult female into the Petri dish 6–24 h before the trial to allow her to habituate to the new surroundings and deposit silk and pheromones, although moisture in the filter paper could deactivate the pheromones in the female silk (e.g., Vlček 1995). We recorded the spiders' behavior from above for 15 min. That period was all that was necessary. If copulation occurred, it ended before that time was up. For recording in terraria, we chose females whose burrows were situated so that it was possible to effectively record the interactions of both spiders. The period of recording depended on the length of interactions; we videotaped until the copulation ended.

We registered courtship latency, courtship duration, copulation duration and copulatory characteristics (number of insertions, number of side shifts, and behavior of the mating spiders). We designated the moment when a male climbed onto a female as the beginning of copulation, and the moment when the spiders physically separated as the end of copulation.

After copulation, we placed females back in their terraria. Through transparent bottoms of the terraria, we observed the cocoon spinning and maternal care. The cocoons appeared to be adhered to the ventral surface of females' abdomens. In an attempt to determine the structure responsible, we used a scanning electron microscope JEOL 6380 LV to examine the ventral surface of females' abdomens (n = 4). After the spiderlings left a female, we removed the soil from the terrarium piecewise to count spiderlings.

We used the program NCSS 2001 (Number Cruncher Statistical System) (Hintze 2006) to test normality of continuous variables and to calculate descriptive statistics (medians and ranges [R] for data with normal distribution, and medians and quartiles [Q_1, Q_3] for data not normally distributed) on courtship latency, courtship and copulation duration, number of insertions, delay between copulation and making cocoons, lengths of guarding periods and number of offspring. As our data set includes multiple observations and is therefore biased, we used the statistical analysis purely for descriptive use.

RESULTS AND DISCUSSION

Courtship.—In the 29 pairs observed in Petri dishes, all males initiated courtship in 1–2 min (median = 0.84, Q_1 = 0.20, Q_3 = 1.94, n = 29) after we placed them in the Petri dishes (courtship latency). The males walked in random trajectories and paid attention to holes in the filter paper bitten by females. They were looking for and finally finding the females (n = 23), or were not active and then the females contacted them first (n = 6) using legs I. After locating females, the males usually started to drum with their legs I and II against the substrate and vibrate with their opisthosomas in a vertical plane for 3 s (n = 26). Vibrations of legs and opisthosomas propagate well through soil and thus are useful for burrowing species. Surprisingly, *T. lutetiana* did not display any behavior commonly known in other wolf spider species: neither palpal drumming nor leg-waving (e.g., Eason 1969). When the males were standing near the female, they jerkily turned towards the females. When standing face to face, the females placed legs I against the males, so females' tarsi I were oriented parallel to the bottom of the Petri dish (Fig. 1). All males contacted females' legs I immediately, using their legs I. After contacting with legs I, they both proceeded to contact with legs II in addition to legs I (Fig. 2) for 2 s. Courtships in Petri dishes lasted nearly 2 min (median = 0.68, Q_1 = 0.48, Q_3 = 1.88, n = 29) (Fig. 3). Then the males went directly up to the dorsal side of the females. A female signaled her readiness for copulation in a quite unusual way. While, for example, a *Trochosa* female presses her legs against her body (Engelhardt 1964), a *T. lutetiana* female never did so, and the females also never produced any vibratory signal. So, her "ready-signal" must be the accurate leg I and II contact with the male, similarly to the "sparring" movements reported in *Hogna helluo* (Walckenaer 1837) (Kaston 1936; Nappi 1965), or *Geolycosa turricola* (Treat 1880) (Miller & Miller 1987). However, all three species differ in duration of those movements and in the further behavior of the pair. The reason for that behavior is that a female is sitting in a dark burrow, and thus a male cannot see her position. Bristowe & Locket (1926) also recorded leg contact in pairs of burrowing wolf spiders.

In terraria, the spiders lived in more natural conditions, and we did not measure the courtship latency as the males sometimes hid in a crevice in the ground and did not move

Figures 1–2.—*Tricca lutetiana*, courtship. 1. Female (down) is shifting legs I against a courting male; 2. Both spiders (male on the right) are touching each other using leg pairs I and II.

for a long time (n = 3 out of 8 males). All males courted intensively: they vibrated with all legs. The females' responses were the same as in Petri dishes; all females lifted their legs, thereby breaking the roof of their burrows and making an entrance for the males. However, how males find the entirely closed underground burrows of females and how they know where to court is still unclear. The males could not detect any females' cues deposited on silk, as no threads appeared on the surface above the burrow. Maybe the males could detect some chemical cues deposited by the females on the ground in the burrow. Because the females are present in the burrows all the time and are probably producing chemical cues continuously, it does not matter that the moisture present in the soil could deactivate those cues. Another possibility is communication via airborne olfaction, as in *Pardosa milvina* (Hentz 1844) (Searcy et al. 1999) and two burrowing *Allocosa* Banks 1900 species (Aisenberg et al. 2010). Contrary to the situation in the Petri dishes, the males in terraria first retreated and then repeatedly continued courtship, drawing close to the female's now open burrow. Therefore, courtships in the terraria lasted notably longer (median = 8.59 min, R = 1.10–24.17, n = 8)

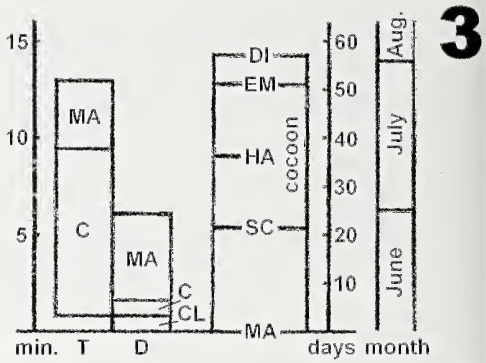


Figure 3.—*Tricca lutetiana*, typical sequence and the median time spent at each stage of reproduction. C = courtship, CL = courtship latency, D = trial in a Petri dish, DI = dispersion of spiderlings, EM = emergence from the cocoon, HA = hatching in the cocoon, MA = mating, SC = spinning the cocoon, T = trial in a terrarium.

(Fig. 3). Finally, all males mounted the females inside the burrow, and the females did not leave the burrow. Consequently, touching, vibrations, and probably chemical cues are the only possible means of communication between males and females of this species, and thus its courtship contains limited visual signaling. It appears that *T. lutetiana* has complex tactile communication during courtship.

Mating.—The males grasped the females' leg pairs I and II using their leg pairs III and IV, so the females stood on their leg pair III and IV. The latter leg pair was spread broadly (Fig. 4). The in-copula position was as in other lycosid species (e.g., Foelix 1996; Stratton et al. 1996); the males waggled their opisthosomas up and down during copulation, similarly to other wolf spiders (e.g., Kaston 1936). However, the act of copulation of *T. lutetiana* was surprisingly dynamic. It was unique to the species that all males showed special movements of their legs. When the males copulated with their left pedipalps (Fig. 4), they stroked the females' opisthosoma in the area of the spinnerets (or on its ventral part) using their left leg I. Simultaneously, a male stroked the female's left leg III using his right leg II (Fig. 4). Several males also moved with their left legs II (n = 13). When copulating with the right pedipalp, the male performed the same movements vice-versa (for a short video clip see http://web.natur.cuni.cz/zoologie/invertebrata). Sometimes, the male started those specific movements during the second (n = 8), third (n = 6), or even fourth (n = 4) insertion. Four females contacted the appropriate males' legs if males did not perform those movements.

In terraria, copulation of *T. lutetiana* always occurred inside the females' burrows (i.e., under the surface). Copulations of burrowing wolf spiders studied up to now almost always proceed at the burrow entrance (e.g., Miller & Miller 1987; Stratton et al. 1996), at the level of the surface. Only a few lycosids copulate inside their burrows: *Allocosa alticeps* (Mello-Leitão 1944) (Aisenberg & Costa 2008), *Allocosa brasiliensis* (Petrunkevitch 1910) (Aisenberg et al. 2007),

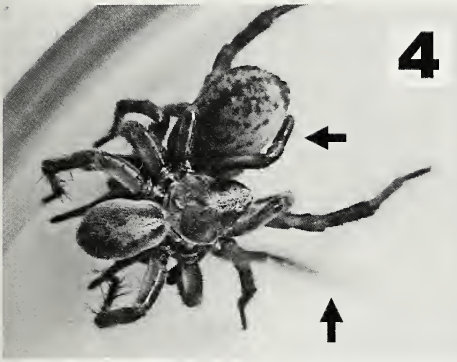


Figure 4.—*Tricca lutetiana*, mating. Insertion of the left pedipalp, male is moving his left I and right II legs (arrows) and opisthosoma.

Allocosa fasciiventris (Dufour 1835) (Fernández-Montraveta & Ortega 1990), and *Xerolycosa mongolica* (Schenkel 1963) (Y.M. Marusik pers. comm.). Copulation inside a burrow perhaps leads to the most important feature of *T. lutetiana*: the peculiar movements in the in-copula position that have not yet been observed in any other wolf spider species. The movements may inform a female that a male is not prey and sexually stimulate her. The former function is supported by the fact that *T. lutetiana* preys in the dark inside the burrow (Dolejš et al. 2008), whereas other burrowing wolf spiders venture out for prey (Nyffeler 2000). The copulation is relatively short, so males probably do not have enough time to produce chemical cues (if the males use any). The latter is why some females "encouraged" the males to initiate movements. The movements seem to be a very important feature, and their hypothetical presence in another lycosid species may solve the unclear taxonomical position of *T. lutetiana*.

When shifting from one pedipalp to the other, the males tapped on the females' opisthosomas. The shifts lasted three to four seconds. We observed six insertions (R = 2–11, n = 31) during copulation. Any subsequent insertion usually lasted longer than the preceding one. Increasing lengths of insertions seem to be a common feature in lycosid copulation, since Montgomery (1903) also observed it. We recorded a male spine erection at the beginning of each palpal insertion (due to increased body pressure during insertion and expansion of the hematodocha [Foelix 1996]). Judging from the male spine erections, there was only a single expansion of the hematodocha per insertion and a single insertion on a side before switching sides. The copulatory pattern of *T. lutetiana* followed those of eleven wolf spiders listed by Stratton et al. (1996). We recorded that not only the males, but also the females, erected their spines (n = 19) during shifting the pedipalp. This movement (together with swiveling females' abdomens so as to bring the epigynum within reach of the male pedipalp, as it was recorded in other lycosids [Bristowe & Locket 1926; Rovner 1971]) revealed that they were not cataleptic, unlike females of e.g., *Trochosa* (Engelhardt 1964) or *Rabidosa santrita* (Chamberlin & Ivie 1942) (Brown 2006). Therefore, it is remarkable that neither males nor females were aggressive toward each other during their cohabitation in the Petri dish (with exception of two females who ate the male before he could begin courtship). No female attacked the male after copulation. That confirms the peaceable behavior of the species observed by Dolejš (2006). If any catalepsy was present in this species, the unique males' leg movement would be of no use.

The copulation in Petri dishes lasted a few minutes (median = 4.35, R = 1.08–9.58, n = 29), similar to a burrowing *Arctosa perita* (Latreille 1799) (Bristowe & Locket 1926). A short copulation is typical for obligate burrowing species and is related to the more primitive copulation pattern, with one insertion on one side (Stratton et al. 1996). Three males cleaned their pedipalps with their chelicerae following copulation. Surprisingly, no males cleaned their pedipalps during copulation, even though Montgomery (1903) and Lopez (1987) considered it a frequent behavior. We never observed the details of the male's sperm induction. After copulation in the terraria, of similar duration to copulations in Petri dishes (median = 2.15, Q_1 = 1.79, Q_3 = 6.72, n = 8), the males left the burrow very quickly. In two cases only, the female also left it (see http://web.natur.cuni.cz/zoologie/invertebrata), but no female attacked a male. Then the females began to repair the broken "roof" of their burrows. They brought small pieces of soil from the bottom of the burrow and stuck them into the open entrance that resulted after the copulation, and secured them with a few isolated threads (n = 8) (see http://web.natur.cuni.cz/zoologie/invertebrata). The females' subterranean lifestyle in enclosed burrows places great restrictions on the reproductive behaviors of both males and females, and may be the underlying cause of the differences between *T. lutetiana* and previously studied lycosids.

Maternal behavior.—Twenty-eight females laid eggs in captivity. Fifteen of them were laboratory mated (86.7% cocoons viable) and thirteen females refused males in the laboratory, so we presume that they had already mated in the field (92.3% cocoons viable). We found that adult females live for two years. The following year (after hibernation), twelve females laid eggs again. Nine of them laid without mating (66.7% cocoons viable) and three females mated in the second year (1 viable cocoon). Thus females are able to store sperm in their receptacula for one year after copulation and need not mate again in the second year of adulthood. All of the females produced only one brood per season (n = 32) at the end of June, three weeks (median = 21 days, R = 3–48, n = 18) after copulation (Fig. 3). Therefore, *T. lutetiana* differs from many other wolf spider species, whose adult females live for one year and produce two cocoons; e.g., *Arctosa cinerea* (Fabricius 1777) (Framenau et al. 1996). Only Fernández-Montraveta & Ortega (1990) found similarly long-lived females, also producing cocoons in two years, in *Allocosa fasciiventris*.

Females always made cocoons in their underground burrows. The cocoons were globular, white, and 3–4.5 mm diam. (year 1, n = 28; year 2, n = 12), as reported Koch (1878). We observed three females during cocoon spinning. Their behavior (see http://web.natur.cuni.cz/zoologie/invertebrata) was similar to that reported by Montgomery (1903), Vlijm (1962), Eason (1964), Engelhardt (1964), and

Table 1.—Cocoon building. Summary of the phases (sensu Montgomery 1903 and Engelhardt 1964) observed in wolf spiders. Time in minutes. SC = spinning a scaffold, BA = spinning a base of the cocoon, MW = spinning a marginal wall on the base, OV = oviposition, CO = spinning a cover of the cocoon, LO = loosening the cocoon from the scaffold, SU = spinning upon the cocoon. * = observed, but without time indication; X = not observed.

Species	SC	BA	MW	OV	CO	LO	SU	Source
Pardosa amentata (Clerck 1757)	*	18	5	*	13	3	*	Vlijm 1962
Pardosa lapidicina Emerton 1885	*	30	*	4–6	25–30	8	16–20	Eason 1969
Pardosa milvina (Hentz 1844)	30	34	5 or X	2–4	12–14	3–4	9–40	Montgomery 1903
Rabidosa punctulata (Hentz 1844)	*	33	13	4–6	20–30	12–25	25	Montgomery 1903; Eason 1964; Eason & Whitcomb 1965
Schizocosa avida (Walckenaer 1837)	*	42	17	3	15	2–5	27	Montgomery 1903
Schizocosa bilineata (Emerton 1885)	*	20	37	5	25	4	24	Montgomery 1903
Schizocosa crassipes (Walckenaer 1837)	* or X	45	14–20	4–5	18–35	2–5	22–25	Montgomery 1903
Tricca lutetiana (Simon 1876)	16	44	X	8	24	4	24	this work
Trochosa spp.	38	65	28	14	27	3	16	Engelhardt 1964

Eason & Whitcomb (1965) (Table 1). The diameter of the cocoon base of *T. lutetiana* was 7 mm, with a denser middle part (diam. 3.5–4 mm) ($n = 3$), but without the marginal wall, contrary to the description of the above-mentioned authors.

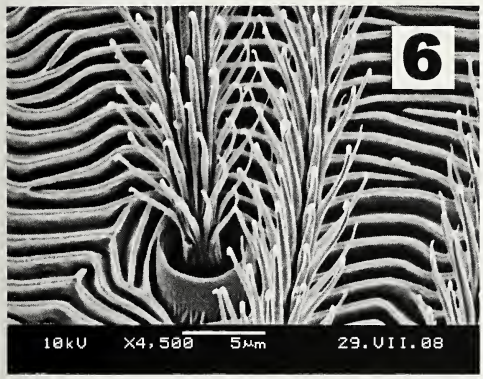
All the females kept their cocoons in their burrows, and they did not leave the burrows in any situation. In about one-third of the observations, females kept the cocoons fastened to their spinnerets, and the cocoons then swung under the opisthosoma. In the remaining observations, females kept their cocoons under the ventral side of their opisthosoma and held them by leg pair IV under the opisthosoma (Fig. 5). That method of cocoon maintenance seems to be a common feature among lycosids, as we observed it in *Alopecosa sulzeri* (Pavesi 1873) (P. Dolejš, pers. obs.), and Montgomery (1903) observed it in *Hogna helluo*. However, while *T. lutetiana* females were moving, the cocoons were in a stable position. We recorded setae (Fig. 6) with hooked endings (Fig. 7) on the ventral part of the females' opisthosomas ($n = 4$). Their function is probably to fasten the cocoon to the opisthosoma. Rovner et al. (1973) discussed the function of the hairs in *Rabidosa punctulata* (Hentz 1844); however, they described the ending of the hairs as "knobbed tips." The explanation of the contrast is in the different magnification used. We examined the hairs of *T. lutetiana* under magnification 4500–12000×, whereas Rovner et al. (1973) studied those of *R. punctulata* with magnification 1000–3000×.

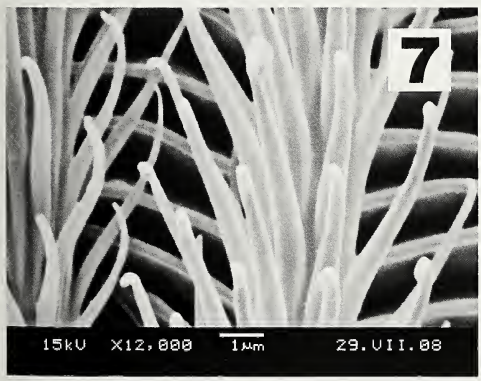
Spiderling emergence.—The juveniles hatched from eggs in the cocoon after 2 wk (median = 15 days, R = 12–19, $n = 29$), in mid-July (Fig. 3). Hatching was obvious from the increase in diameter of the cocoon, which grew to about 1–1.5 mm. We did not investigate the embryonic and postembryonic stadia in the cocoons. The juveniles left the cocoon through a cleft in the seam after a month (median = 31 days, R = 24–36, $n = 28$), since the females spun the cocoons (in accordance with Eason [1964]) at the end of July (Fig. 3). The juveniles then climbed onto the females' opisthosomas, where they occupied the whole opisthosomal surface; they did not occupy her carapace, unlike some other wolf spiders (e.g., Montgomery 1903; Eason 1964; Engelhardt 1964; Rovner et al. 1973). Females stayed with them in the burrows for nearly one week (median = $Q_1 = Q_3 = 6$ days, $n = 28$) (Fig. 3), similarly to most wolf spiders (e.g., Nielsen 1932; Eason 1964; Engelhardt 1964; Foelix 1996).

The females with cocoons or spiderlings attached to their bodies caught prey in their burrows ($n = 32$). That disagrees with the statement of Nyffeler (2000), who concludes that guarding females of burrowing species do not feed, whereas those of free-moving species do. Most burrowing spiders only prey outside the burrows (Nyffeler 2000), whereas *T. lutetiana* uses its burrows for hunting (Dolejš et al. 2008). On the one hand, females of *T. lutetiana* carrying cocoons or juveniles have a supply of food without having to leave the burrows. On the other hand, the supply of food under the ground is not probably very rich, and so the females have to take every opportunity to feed.

The females with spiderlings on their opisthosomas left their enclosed burrows in the evening and at night ($n = 28$) at the beginning of August (Fig. 3). While spherical openings were visible on the soil surface, the burrows remained undisturbed and their walls did not collapse. That suggests that the females were leaving their burrows very gently; otherwise they would damage the walls, since the walls did not benefit from the support of a silk lining. The females then stayed on the surface near their former burrows for one day until all the juveniles left their opisthosomas ($n = 22$). All the juveniles left the females on the same day. The last juveniles that remained on the females' opisthosomas did not occupy the ventral part of the opisthosomas anymore. After leaving the females, the juveniles searched for cracks in the ground to hide. When the last spiderlings left, the females hid under a stone or underground and made a new, shallow, bowl-like or spherical burrow reaching a depth of 1 to 1.5 cm. Females reared two-dozen (median = 24, R = 7–46, $n = 32$) spiderlings. That is a relatively small clutch size, among burrowing wolf spiders comparable to only a few burrowing lycosids; e.g., *Geolycosa xera archboldi* McCrone 1963 (Marshall 1995).

Four females behaved quite strangely. They did not leave the burrows, and their spiderlings spread out underground from the mothers' burrows. That was obvious because the spiderlings disappeared from the burrow while the females remained inside the burrows. We saw neither females nor spiderlings on the surface, and we found the spiderlings underground close to their mothers' burrows. Normally when a female left the burrow, we could find the spiderlings underground in all parts of the terrarium. This observation documented that an alternative means of dispersing exists.





Figures 5–7.—*Tricca lutetiana*, cocoon keeping. 5. Female is carrying a cocoon under her opisthosoma using legs IV; 6. Pinnate setae on the ventral part of female's opisthosoma; 7. detail of the setae with hooked endings.

Conclusion.—The subterrestrial life of *Tricca lutetiana* influences all its reproductive behavior. As mating occurs underground, the spiders communicate via vibrations and contacts, even during copulation. The sit-and-wait feeding strategy inside the burrow places restrictions on reproduction of this species. Probably because of the low food supply underground, females produce only one cocoon per year. For the same reason, females catch prey in the burrow even when carrying spiderlings.

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Description of the female of *Orsolobus pucara* Forster & Platnick 1985, with comments on the functional morphology of the female genitalia in Dysderoidea (Araneae: Dysderoidea: Orsolobidae)

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Abstract. The female of *Orsolobus pucara* Forster & Platnick 1985 is described and its genitalia examined using the scanning electron microscope (SEM). A small phylogenetic matrix with female genital and sexual behavior characters was made with the aim to study the evolution of these characters in the superfamily Dysderoidea. This is the first time that the female genitalia of a species of the family Orsolobidae have been studied in detail with SEM. The anterior portion of the female genitalia is a sclerotized structure with gland ducts and sites for muscle attachments. The posterior portion has a membranous receptaculum and a sclerotized plate that serves as attachment for muscles. We discuss the probable function of genital characters in a phylogenetic context. The anterior sclerotized elements of the female genitalia of some Dysderidae, Orsolobidae and Oonopidae species and the anterior receptaculum in the Segestriidae seem to be homologous structures because of the presence of gland ducts and sperm. However, both of these characteristics are lost in some species of these families, the anterior portion of the female genitalia being transformed into a highly modified structure serving mainly as attachment for muscles implicated in sexual behavior mechanisms.

Keywords: Character evolution, complex genitalia, reproductive behavior, spiders, taxonomy

The family Orsolobidae Cooke is a group of haplogyne spiders with six eyes that can by distinguished by the presence of an elevated tarsal organ (Fig. 7D). These active hunting spiders are distributed in eastern and western Australia, New Zealand, South Africa, Argentina, Falkland Islands, Chile and Brazil (Forster & Platnick 1985; Griswold & Platnick 1987; Platnick & Brescovit 1994; Brescovit el al. 2004; Baehr 2009).

The Orsolobidae, together with the Dysderidae, Oonopidae and Segestriidae, are grouped in the haplogyne superfamily Dysderoidea by the occurrence of a second portion of the internal female genitalia associated with the posterior wall of the bursal cavity (Forster & Platnick 1985; Ramírez 2000). Although the female genitalia of many haplogyne spiders are simple, such as in the Filistatidae and Caponiidae, the genital structures of other families (among them the Orsolobidae and Oonopidae) appear rather complex (Burger & Kropf 2007). In some species the anterior section of the female genitalia (AFG henceforth) has a very complex organization. It has been proposed that the degree of complexity might involve mechanisms of cryptic female choice, sperm dumping, and genital organization similar to the entelegyne condition (Uhl 2000; Huber 2002; Burger et al. 2003, 2006; Huber et al. 2005; Burger 2007; Burger & Kropf 2007). The oonopid genus *Scaphiella* Simon 1891 is in fact functionally entelegyne, since they have separate copulatory and fertilization openings and ducts (see Burger 2009). The same condition occurs in the diverse genus *Escaphiella* Platnick & Dupérré 2009 (Platnick & Dupérré 2009).

Although Forster & Platnick (1985) illustrated the diversity of female genital structures in the Orsolobidae, the fine structure of this group is unknown, thus precluding more detailed functional hypotheses. Also, homologies are difficult to explore when comparing, for example, the simple genitalia of segestriid genera like *Segestria* Latreille 1804 or *Ariadna* Audouin 1826 with the complex configurations found in oonopids like *Antoonops* Fannes & Jocqué 2008 or *Opopaea fosuma* Burger 2002 (probably to be transferred to another genus in the future). For details compare fig. 2b in Grismado 2008 with fig. 3 in Burger et al. 2003).

With this work we wish to provide the first SEM images of the female genitalia in the family. Also, we compare the morphology of the female genitalia of *O. pucara* with other species of Dysderoidea. We used published data about the functional mechanisms of the genitalia across the superfamily to infer similar patterns in *O. pucara* and the Orsolobidae in general, to detect possible homologies and to discuss the evolution of the female genital characters. Detailed images of the male palp are also presented, and other anatomical structures of the female are illustrated.

METHODS

Specimens are deposited in the collection of arachnids of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (MACN-Ar, Cristina Scioscia).

The format of descriptions and morphologic terminology follows in general Forster & Platnick (1985). In describing the female genitalia, we used the criterion followed by Platnick et al. (1999) for naming structures situated anteriorly or posteriorly to the uterus externus. Abbreviations used for eyes and legs are standard in arachnology. Measurements are in millimeters. After dissection, the female genitalia were digested in hot KOH and mounted in temporary preparations with lactic acid. The male palp was cleared with clove oil. A camera lucida mounted on a compound microscope (Olympus BH–2) was used to make drawings. Photographs of preserved spiders were made with a digital camera (Nikon DXM1200) mounted on a stereoscopic microscope (Nikon SMZ 1500). The focal planes were combined with Helicon Focus 3.10.3 (online at http://helicon.com.ua/heliconfocus/). Scanning electron micrographs were taken under high vacuum with a FEI XL30 TMP after critical point drying and Au–Pd coating. A small phylogenetic matrix with genital and sexual behavioral

Table 1.—Terminal included in the phylogenetic analysis and the data source where the characters were constructed.

Family	Terminal	Data source
Caponiidae	*Nops* MacLeay 1839	Izquierdo & Labarque pers. obs.
Segestriidae	*Ariadna boesenbergi*	Grismado 2008; Izquierdo & Labarque pers. obs.
Dysderidae	*Dysdera erythrina*	Uhl, 2000
	Hapactea lepida (C.L. Koch 1838)	Burger & Kropf 2007
Orsolobidae	*Orsolobus pucara*	Forster & Platnick 1985; Izquierdo & Labarque pers. obs.
	Osornolobus Forster & Platnick 1985	Forster & Platnick 1985
Oonopidae	*Scaphiella hespera* Chamberlin 1924	Burger 2009
	Antoonops corbulo Fannes & Jocqué 2008	Fannes & Jocqué 2008
	Silhouettella loricatula (Roewer 1942)	Burger et al. 2006
	Opopaea fosuma	Burger et al. 2003
	Orchestina (sp.1)	Izquierdo & Labarque pers. obs.; Burger et al. 2010
	Orchestina (sp. 2)	Izquierdo & Labarque pers. obs.
	Grymeus	Burger 2010
	Lionneta	Burger 2010
	Myrmopopaea	Burger 2010

characters includes morphological and behavioral characters described in the literature and from our personal observations (Fig. 8). The terminals and sources are listed in Table 1. The phylogenetic tree was taken from the previous analyses of Platnick et al. (1991) and Ramírez (2000). The Oonopidae was considered monophyletic, but without any internal structure, except for two groups supported by potential evidence: the *Lionneta* Benoit 1979, *Grymeus* Harvey 1987 and *Myrmopopaea* Reimoser 1933 clade (see Burger 2010) and the genus *Orchestina* Simon 1882 (jumping oonopids). Characters were mapped on this tree using TNT (Goloboff et al. 2008). The aim of this small analysis is to explore the evolution of the female genitalia characters in the Dysderoidea; a full reanalysis of dysderoid relationships is beyond the scope of this contribution.

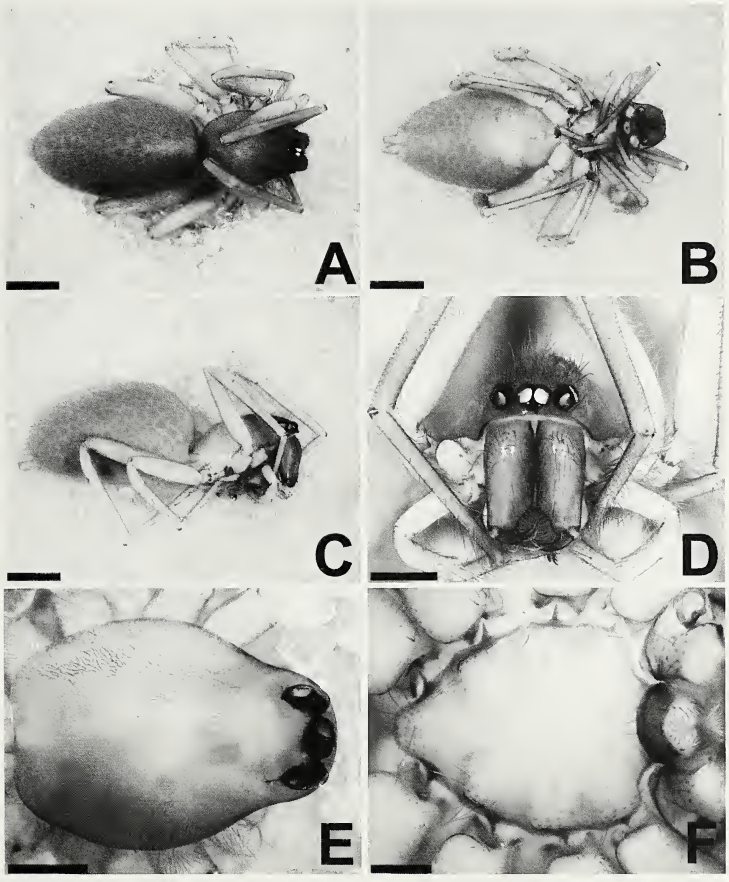
SYSTEMATICS

Orsolobus pucara Forster & Platnick 1985 (Figs. 1–7)

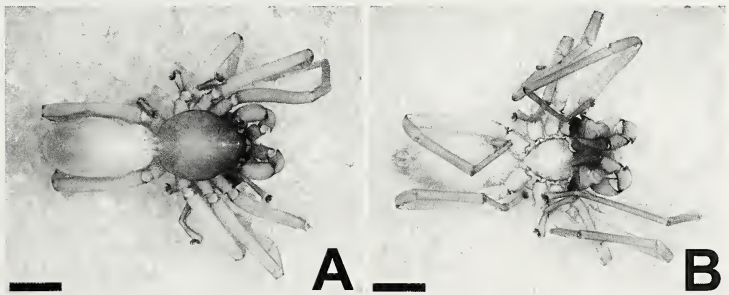
Female diagnosis.—Easily distinguished from other females of the genus by the shape of the median rod, bifurcated at the tip and with a flattened projection directed ventrally (Figs. 3 A, B).

Description.—(MACN-Ar 16120). Total length 3.47, carapace 1.40 wide, opisthosoma 1.80 wide. Leg length I: 6.49, II: 5.90, III: 4.93, IV: 6.44; palp length 2.08. Carapace pale orange with several setae in the surface (Fig. 1); legs and maxillary endites pale yellow, sternum and labium pale orange. Opisthosoma pale yellowish with many dots of pigment, visible by transparency through the cuticle (Figs. 1A–C). Spinnerets yellow. ALE and PLE contiguous, PME–ALE separation 0.08. Chelicerae length 1.02 with two teeth on promargin (contiguous) and two on retromargin (slightly separated) (Fig. 7A). Sternum 1.03 long, 0.87 wide, more widened between coxae 2 and 3, sternum with cuticular projections toward coxae (Fig. 1F). Spination: Leg III: Tibia p 0-1-0, r 0-1-0, v p1ap; metatarsus p 0-1-1, r 1ap (displaced to dorsal), v 2ap. Leg IV: Tibia r 1ap, v 2ap; metatarsus p 1-1-1, r 0-1-1, v p1-p1-2. Palp: Tarsus d p1, p 1, v 2ap. Tarsal organ with about ten cuticular lobes and two rounded receptors on Leg I (Fig. 7D) and about ten cuticular lobes and one (maybe two) receptor on leg IV. Retroclaw and proclaw with fifteen teeth on both outer and inner margins (Fig. 7C). Trichobothrial socket with proximal hood at the same level as the cuticle and with the same sculpture (Fig. 7E). Distal hood very short and with same sculpture as cuticle. Base of the trichobothrial seta slightly swollen and with oblique rings (Fig. 7E). AFG heavily sclerotized, formed by only one anterior median plate (mp, Fig. 3A) with four basal spurs, two of them directed dorsally and two ventrally. Between them arises the anterior median rod (mr), which bears numerous gland ducts near its base (Figs. 3C, 4C, E). The tip of the median rod is bifurcated and has several scars corresponding to the places of muscles attachments (Fig. 4D). The median rod has a flattened projection directed ventrally that may also bear muscle insertions (Fig. 3B). Posterior part of the female genitalia (PFG) with a membranous posterior receptaculum formed by a tube–like section that ends in a sack structure. Between them are two sclerotized plates (Fig. 3A, asterisk on Fig. 3B) that may act as supporting structures for the receptaculum or as attachments for muscles that control the aperture of these structures. External surface of the sack structure with many gland ducts formed by short bases (BS) and distal piriform caps (DC) (Fig. 5A). The gland ducts are sparsely distributed or grouped in two or three on the receptaculum surface and communicate into the lumen through simple pores (Figs. 5A, B). There is a "posterior plate" (pp, Figs. 3A, 4A) in close connection with the AFG. The posterior plate has a convex shape in the median line and extends toward both sides, acquiring a flattened shape (fa, "flattened lateral apodemes", Fig. 4B). The position of the uterus externus has been unknown until now. We found that it is located between the anterior median plate of the AFG and the posterior plate of the PFG (Figs. 3A, B, 4B).

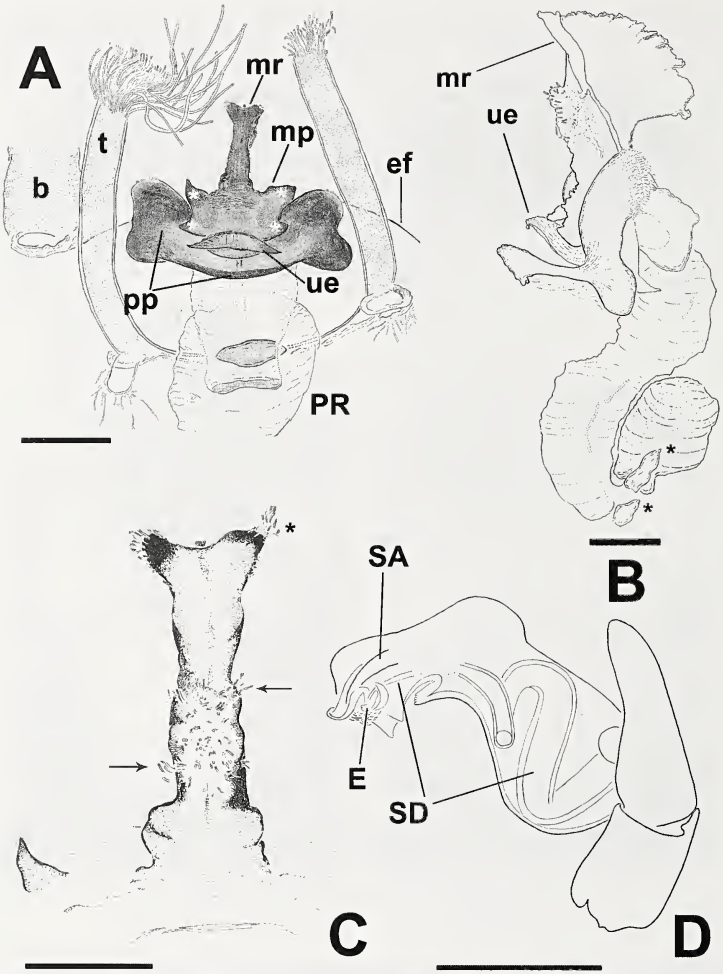
Variability.—We have examined the female genitalia of two additional females from Neuquén and Rio Negro provinces (Argentina), one of them collected together with two males. The tip of the median rod and the size of the gland region differ in both specimens, but the morphology of the other plates does not vary. However, relative positions of the plates may be slightly variable, making the immediate determination



Figures 1 A–F.—*Orsolobus pucara* (MACN-Ar 16120). Female. A. Habitus dorsal; B. Habitus ventral; C. Habitus lateral; D. Eyes anterior; E. Dorsal shield of opisthosoma; F. Sternum. Scale bars: A–C = 1 mm, D, E = 0.5 mm, F = 0.25 mm.



Figures 2 A, B.—*Orsolobus pucara* (MACN-Ar 16567). Male habitus. A. Dorsal; B. Ventral. Scale bars: 1 mm.

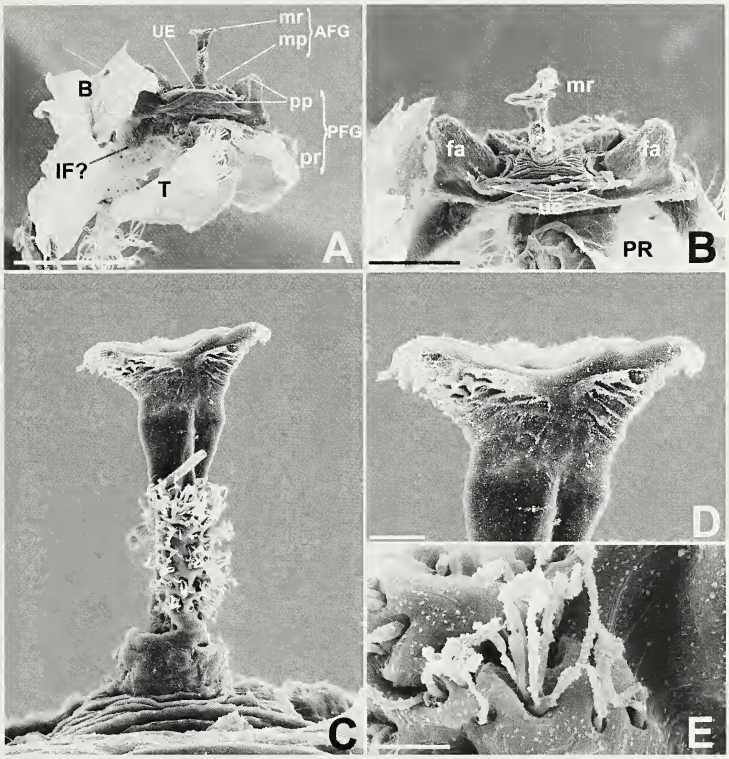


Figures 3 A–D.—*Orsolobus pucara* (MACN-Ar 10873). Genitalia. A–C. Female vulva. A. Dorsal view; B. Lateral view, asterisk on the two sclerotized plates; C. Anterior median rod, arrowheads to the gland ducts, asterisk on rest of digested muscles. D. Male palp, left prolateral view. Abbreviations: b = booklung, pp = posterior plate, E = embolus, ef = epigastric furrow, mp = median plate, mr = anterior median rod, PR = posterior receptaculum, SA = spine-shaped apophysis, SD = spermatic duct, t = tracheal trunk, ue = uterus externus. Scale bars: A = 0.25 mm, B, C = 0.1 mm, D = 0.5 mm.

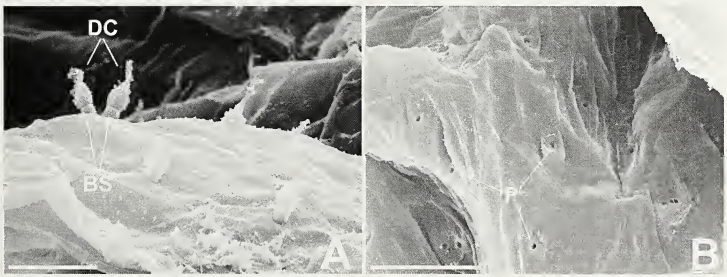
of the species difficult. For correct determination, it is necessary to dissect and digest the genitalia and then observe the preparation from several points of view.

Male.—Described by Forster & Platnick (1985). We provide an additional description of the palp of one male (MACN-Ar 16567) collected together with several females. Internal course of the spermatic duct (SD) as in Fig. 3D. Embolus (E) short, with a wide aperture at the tip (Fig. 6B). The base of the embolus seems to originate from a fold of a striated laminar membrane (LM Figs. 6B, C). Spine-shaped apophysis (SA, Figs. 6B, C) close to the dorsal lobe (DL, Figs. 6C, D). Dorsal subterminal lobe spine-shaped, ventral subterminal lobe slightly flattened (DSL & VSL, Fig. 6A).

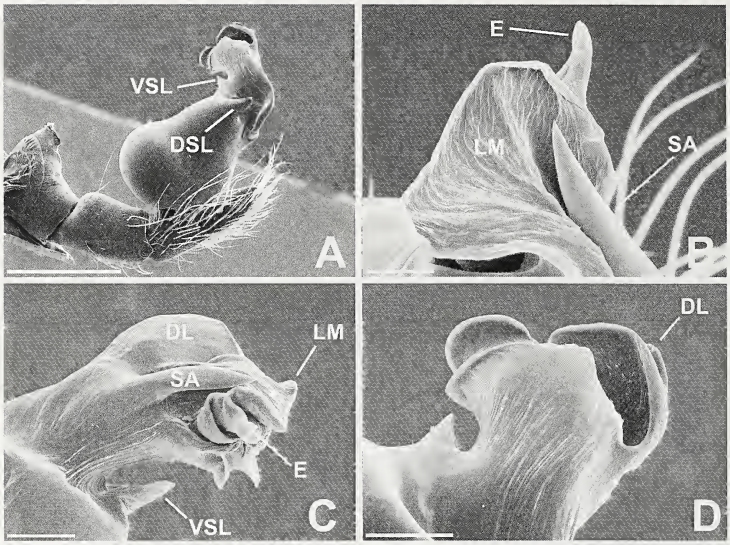
Other material examined.—ARGENTINA: *Neuquén Province*: Cerro Bayo, 1304 m, 40.74796°S, 71.59779°W, March 2005, V. Werenkraut, pitfall traps (cod. M3S5M05), 2 males



Figures 4 A–E.—*Orsolobus pucara* (MACN-Ar 10873). Internal female genitalia. A. Entire dorsal view; B. Anterior portion in anterior view; C. Anterior median rod; D. Tip of the median rod showing the points of muscle attachments and rest of digested muscles; E. Gland ducts on the base of the median rod. Abbreviations: AFG = anterior portion of the female genitalia, B = booklung, pp = posterior plate, EC = external cuticle, fa = flattened apodemes, IF? = interpulmonary fold?, mp = median plate, mr = median rod, PFG = posterior portion of female genitalia, PR = posterior receptaculum, T = tracheal trunk, ue = uterus externus. Scale bars: A = 0.5 mm, B = 0.2 mm, C = 0.05 mm, D = 0.01 mm, E = 0.01 mm.



Figures 5 A, B.—*Orsolobus pucara* (MACN-Ar 10873). Posterior receptaculum. A. External surface showing the gland ducts; B. Internal surface showing the pores of the gland ducts. Abbreviations: BS = base of the gland duct, DC = distal cap of the gland duct, P = pores. Scale bars: 0.02 mm.



Figures 6 A–D.—*Orsolobus pucara* (MACN-Ar 16567). Left male palp. A. Retrolateral view; B. Tip of the copulatory bulb in dorsal-apical view; C. Ditto in prolateral view; D. Ditto retrolateral view. Abbreviations: DL = dorsal lobe, DSL = dorsal subterminal lobe, E = embolus, LM = laminar membrane, SA - spine-apophysis, VSL = ventral subterminal lobe. Scale bars: A = 0.5 mm, B = 0.05 mm, C, D = 0.1 mm.

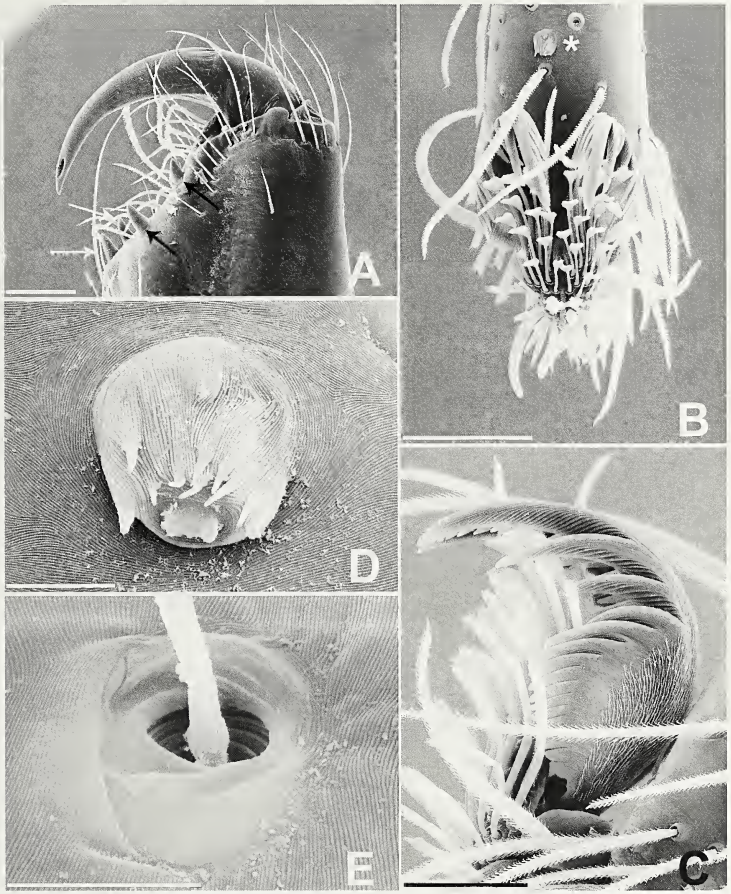
(MACN-Ar 19559); same data January 2006 (cod. M3S5E06), 1 female (MACN-Ar 19560); *Rio Negro Province*: Cerro López, 1502m, 41.09948°S, 71.55801°W, March 2006, V. Werenkraut, pitfall traps (cod. M1S8M06), 1 female (MACN-Ar 19558). CHILE: *Región IX, Cautín Province*: Huerquehue National Park, Laguna Toro, in *Nothofagus* (Nothofagaceae)-*Araucaria* (Araucariaceae)-*Chusquea* (Poaceae) forest, 995m, 39°08′18.7″S, 71°42′30.9″W, 7 February 2005, M. Ramírez & F. Labarque, 1 female (MACN-Ar 16120), voucher codes ARAMR001025; same data 1 male and 2 immature (MACN-Ar 16568); 1 female (MACN-Ar 16570) voucher code ARAMR001026, preparation code MAI-137; 1 female (MACN-Ar 10873), voucher code ARAMR000999, preparation codes MAI-99, 124, 138–140; 1 male and 1 female (MACN-Ar 16567), male voucher code ARAMR000972, preparation codes MAI-58, 69, female voucher code ARAMR000971, preparation codes MAI-23, 63–68, 78; 1 male (MACN-Ar 16571), voucher code ARAMR001021, preparation code MAI-128; Villarica Natl. Park, sector Quetrupillén, in forest of *Araucaria*, *Nothofagus* and *Chusquea*, 1280m, 39°27′42.1″S, 71°50′44.2″W, 8 February 2005, 1 male and 3 immature (MACN-Ar 16569), M. Ramírez & F. Labarque.

Distribution.—Previously known from Argentina, Neuquén Province, here reported for Rio Negro Province and from Chile, Cautín Province (Región IX).

Natural history.—*Orsolobus pucara* was captured beating the vegetation in a *Nothofagus* and *Araucaria* forest, especially on *Chusquea* bamboos (Ramírez & Labarque pers. obs.) in Chile and with pitfall traps in Neuquén and Río Negro Provinces (Argentina).

DISCUSSION

Female genitalia, functional morphology.—The peculiar morphology of the anterior female genitalia appears to be adapted for muscle attachment. The places for muscle attachment seem to be restricted to the tip of the median rod and its ventral projections and to the flattened apodemes of the posterior plate. Forster & Platnick (1985) have noted that the lumen of the median rod of some species of Orsolobidae is sometimes heavily charged with sperm. The presence of different gland types in the anterior and posterior portions of the genitalia has been taken as indicative of two functionally different sites for sperm storage in the dysderid *Dysdera erythrina* (Walckenaer 1802) (Uhl 2000). These glands would produce secretions generating different conditions of sperm storage, although other secretions might be transferred by the male together with the spermatozoa (Burger & Kropf 2007). The presence of gland ducts in the anterior median rod of *Orsolobus pucara* suggests some storage function as well, and therefore a double function: attachment for muscles and sperm storage. Some of the muscles in the anterior portion of the female genitalia could be implicated in mechanisms of sexual selection, as occurs in other families. For example, the muscles M3, M4 and M7 can move some plates, which leads to the closing of the uterus externus in *Triaeris stenaspis* Simon 1891; whereas in *Brignolia recondita* (Chickering 1951) the muscle M3 seems to enable females to move a bulge close to



Figures 7 A–E.—*Orsolobus pucara* (MACN-Ar 16567). Female. Left chelicera. A. Posterior view, black arrowheads to the retromarginal teeth, white arrowheads to the promarginal teeth. B–E. Left leg I structures. B. Tarsal claws in dorsal-apical view, asterisk on the distal tarsal organ; C. Claws in retrolateral view; D. Tarsal organ; E. Metatarsal trichobothrial socket. Scale bars: A–C = 0.1 mm, D, E = 0.01 mm.

the genital opening, which may lead to the ejection of sperm (Burger 2009, under *Opopaea recondita*).

In species of the genera *Myrmopopaea*, *Grymeus* and *Lionneta*, the surface of the posterior receptaculum is pervaded with papillae that resemble those present in the genital structures of water mites (Burger 2010). Likewise, these papillae are present in the segestriid genus *Ariadna* (P. Michalik pers. comm.). Apparently, the papillae might have a function in osmoregulatory processes and could be involved in sperm activation (Burger 2010). However, the gland ducts on the posterior receptaculum of *Orsolobus pucara* are slightly different compared with these species, hence its involvement in osmoregulatory processes is still unclear. Similar gland ducts have been observed in the oonopid *Unicorn catleyi* Platnick & Brescovit 1995 (M.A. Izquierdo pers. obs.).

Phylogenetic context.—If the female genitalia of all Dysderoidea are compared in an hypothetical evolutionary context with the hope of identifying homolog structures (Fig. 8), Segestriidae and almost all the Dysderidae fit well with the notion of a typical Dysderoidea (that is, well delimited anterior and posterior receptacles), while the Orsolobidae and Oonopidae have complex anterior female genitalia with bizarre sclerotized elements. However, it is still possible to find similar structures and infer common mechanisms. The median

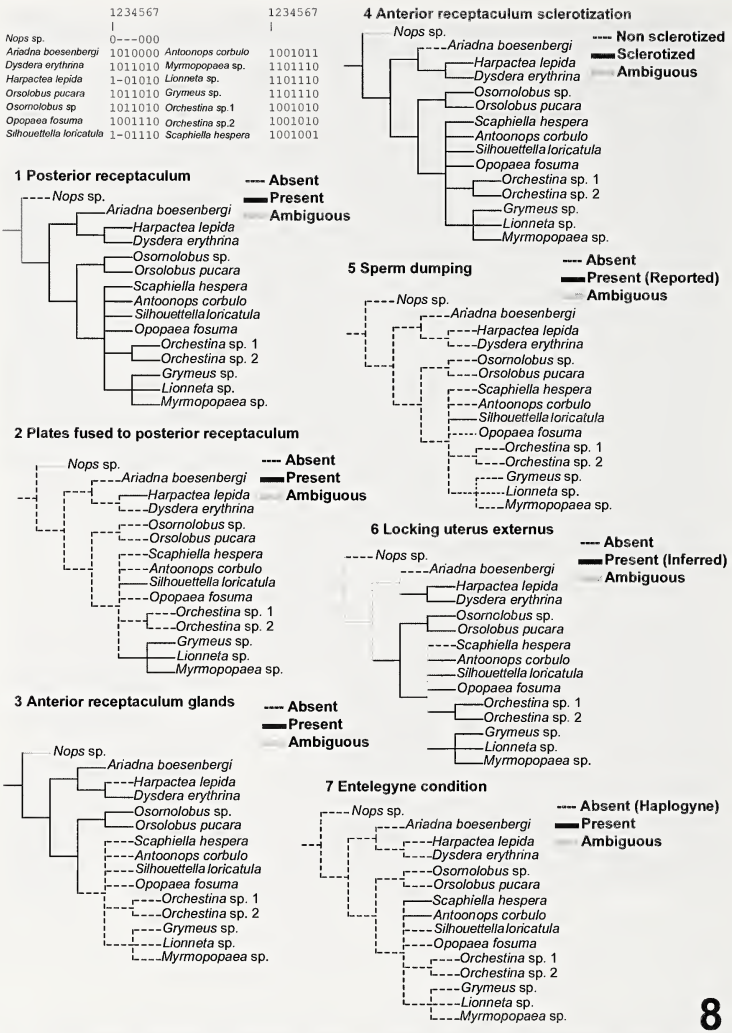


Figure 8.—Data matrix (upper left corner) and optimization for seven genital and sexual behavior characters.

rod and the lateral apodemes of the posterior plate in *Orsolobus* are very similar to other species of Dysderoidea (compare Fig. 3A with fig. 2 in Burger & Kropf 2007 and fig. 3 in Burger et al. 2006). The presence of gland ducts and sperm inside the anterior median rod suggests that these and similar structures in the Oonopidae and other Orsolobidae are homologous with the membranous anterior receptaculum found in Dysderidae and Segestriidae (see Grismado 2008 figs. 1A, 2A, 8H–O; Uhl 2000). As Forster and Platnick (1985) mention, there is a tendency for the storage function of the anterior genitalia to become reduced as the posterior receptaculum becomes larger. The absence of gland ducts in the oonopids analyzed here (Character 3, Fig. 8) and the sclerotization of the anterior receptaculum (Character 4, Fig. 8) seem to indicate a switch in the function of the anterior receptacle, from sperm storage to attachment of

muscles involved in copulatory and post-copulatory mechanisms. Gland ducts in the anterior female genitalia have recently been observed in undescribed oonopids from the molles spiny group (C.J. Grismado pers. comm.), *Heteroonops* Dalmas 1916 (N.I. Platnick & N. Dupérré pers. comm.), and in *Unicorn catleyi* (M.A. Izquierdo & Rubio unpubl. data).

All the Dysderoidea included in the matrix except *Ariadna boesenbergi* Keyserling 1877 and *Scaphiella hespera* Chamberlin 1924 have a mechanism of uterus externus locking (Character 6, Fig. 8) that would prevent the spermatozoa from getting into it during copulation (Burger et al. 2006). The locking mechanism is possible because of the combined presence of muscles and sclerotization of the anterior receptaculum (or part of it) and additional plates, both serving as attachments for those muscles. When the muscles contract, the plates contact each other and lock the uterus (for detailed morphology see Uhl 2000; Burger & Kropf 2007; Fannes & Jocqué 2008; Burger 2009, 2010; Burger et al. 2003, 2006, 2010). The absence of sclerotization in the female genitalia of the segestriid *Ariadna boesenbergi* suggests that this mechanism is not present in this species and probably in the whole family. The absence of locking mechanism in *Escaphiella hespera* is consistent with the development of a unidirectional sperm flux in the genitalia, a configuration typical for the Entelegynae (Character 7, Fig. 8). In *E. hespera* there are two ducts: one of them connects the copulatory opening with the posterior receptaculum and the other connects the posterior receptaculum with the uterus externus (Burger 2009). This configuration suggests that the locking mechanism of the uterus externus is not necessary in this species, since the males have no direct contact with this structure during copula. The locking mechanism has been reported for another group of gamasomorphine species (not analyzed here; see Burger et al. 2006), and it is probably present in the genus *Orchestina* as well (Burger et al. 2010; Izquierdo & Labarque pers. obs.).

Sperm dumping is a common means of cryptic female choice by which the females discard sperm from current or previous matings (Eberhard 1996). In Dysderoidea sperm dumping has been reported only in *Silhouettella loricatula* (Roewer 1942) (Burger 2007; Burger et al. 2006). However, this mechanism of cryptic female choice has been suggested for other gamasomorphine oonopids of the genera *Opopaea* and *Xyphinus* Simon 1893, *Gamasomorpha* Karsch 1881, *Grymeus*, *Lionneta* and *Myrmopopaea* (Burger et al. 2003; Burger 2010). This behavior seems possible only with the combined presence of sclerotized structures and muscles in the female genitalia.

ACKNOWLEDGMENTS

We sincerely thank Barbara Baehr, Barbara Knoflach and Matthias Burger for critical corrections on the manuscript. Martín Ramírez, Cristian Grismado and Norman Platnick provided useful comments on early versions of the paper. We thank the Argentinian Administración de Parques Nacionales for the autorization to work in the Calilegua National Park and Reserva Natural Otamendi, where *Orchestina* specimens were collected. Fabián Tricarico offered technical support at the SEM laboratory. The study was financed by grants from the following organizations: National Science Foundation (for the Assembling The Tree of Life: Phylogeny of spiders, grant EAR-0228699 and for a Planetary Biodiversity Inventory of the spider family Oonopidae, grant 0613754), ANPCyT (grant PICT-2007-01393) and CONICET (grant PIP 112-200801-03209 and doctoral fellowships for M.A.I. and F.M.L.). TNT was made available thanks to the sponsorship of the Willi Hennig Society.

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Platnick, N.I., C.J. Grismado & M.J. Ramírez. 1999. On the genera of the spider subfamily Otiothopinae (Araneae, Palpimanidae). American Museum Novitates 3257:1–25.

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Opilionological Record – a chronicle of harvestman taxonomy. Part 1: 1758–1804

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Abstract. Based on a firsthand parsing of the original literature, a Zoological Record-style tabulation of all nomenclatural acts regarding species of the order Opiliones is presented for the interval between 1758 and 1804. A total of 52 species was described as new, 14 of which are not Opiliones or remain unrecognizable (nomina dubia), six species have been synonymized (one revalidated), in all resulting in 33 valid species of Opiliones. Four genera were established, although no more than three were used simultaneously. The family Phalangita (Phalangiens) was described and coincides with the modern use of the order Opiliones. Of the current four recognized suborders of Opiliones, three (Cyphophthalmi, Eupnoi and Dyspnoi) were recorded. Laniatores remained unknown. A checklist is given for the order Opiliones up to 1804.

Keywords: Opiliones, 18th century, nomenclature, checklist

The early taxonomic history of the arachnid order Opiliones is not always accurately documented in the literature, where most authors only cite secondhand information with notable mistakes and omissions. The Zoological Record, which started to tabulate taxonomical data from 1864, is an excellent resource for later periods, but the 19th century is abbreviated and full of omissions. Therefore, a recension of this early output is of paramount importance for reliably establishing a systematic catalogue.

For this paper, I have parsed all references between 1758 and 1804, extracting all nomenclatural acts relevant for the species treated in the period. The chosen landmarks have been the starting point of the modern nomenclature (Linnaeus 1758) with the description of the very first species, *Phalangium opilio*, and the year 1804, the date of issue of two important papers (Latreille 1804; Hermann 1804) and the first solid appearance of the Cyphophthalmi in the literature.

Use of name Palpatores as a monophyletic group including Eupnoi + Dyspnoi has recently been both reaffirmed (e.g., Giribet et al. 2010) and denied (e.g., Giribet et al. 1999, 2002). I have used a safer, middle course here by considering Opiliones divided into four suborders, with Eupnoi and Dyspnoi taken separately.

METHODS

A chronological list of references in taxonomy of Opiliones from 1758 to 1804 is given in full as Table 1, without abbreviations. A table has been built charting the number of described species, including synonymies and revalidations, trying to mimic the Zoological Record style (Table 2). Also included are six numerical columns containing 1) increment to described species; 2) increment to the species considered junior synonyms; 3) increment to revalidated species, i.e., species taken out of synonymy; 4) increment of invalid species (not junior synonyms), because they do not belong to Opiliones, or because they are nomina nuda, unrecognizable and not listed in the official species list. The fifth column represents the total value to be added to the general count, adding columns 1 + 3 − 2 − 4. All these five columns can have values of 0 or 1. The sixth column is the cumulative count of valid species; values are integers.

I give a historical account, detailing the main results of the works included in the period. In that section, the original spellings are retained, even if they conflict with modern usage, e.g., *Phalangium Opilio*, with capital O as used by Linnaeus, even though species names should be spelled with lower case o (International Code of Zoological Nomenclature [ICZN], Art. 28). Likewise, in that section only, I have conserved the original *Trogulus nepæformis*, using the ligature -æ, which should be corrected to −ae (ICZN, Art. 32.5.2). In the checklist (Table 3), I have used the corrected forms *Phalangium opilio* and *Trogulus nepaeformis*.

RESULTS

A total of 22 references is listed in Table 1, ten written in French, nine in Latin, and three in German (although there is a mix of languages in some, with parts in Latin as well). The new taxa, combinations, and synonymies are tabulated in Table 2. A non-exhaustive list of species described in *Phalangium* that are not currently included in Opiliones is given in Table 4.

A total of 52 species was described as new, of which 14 (almost 27%) are unrecognizable or not Opiliones (a miscellany including other arachnids and even marine arthropods), a 15th (not counted among the 52) has been transferred from *Acarus* (see Table 4). Of the remaining 38 species, six have been synonymized (but 1 revalidated), leaving a total of 33 valid species of Opiliones by the end of 1804 (1 Cyphophthalmi, 26 Eupnoi, and six Dyspnoi). Of these 33 species, 14 were synonymized in later periods, that is, almost 60% (19 out of 33) of the species described in this period are valid now, 200 years later. Some had a great longevity and were synonymized only much later; for example, *Opilio hispidus* took more than 100 years to be synonymized with *Phalangium horridum*.

As expected, the bulk of the described species of *Phalangium* and related genera is European. Of the 52 new species, six do not have explicit provenance or are marine, 15 are from France, 13 from Germany, six from either Sweden/Denmark/Norway, two from Switzerland, one each from England, Romania, Russia and Slovenia, one widespread Holarctic, three Neotropical and two Indo-Malayan (see Table 2 for details). By the 1770s the first synonymies started to be proposed, and in the 1790s others followed, including Olivier (1792) and Latreille (1798), who proposed two conflicting junior synonyms for *Phalangium opilio*.

Table 1.—List of the works published between 1758–1804 carrying nomenclatural acts on Opiliones.

1758

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Tomus 1. Laurentius Salvius, Stockholm. Pp. [iv] + 1–824. [ICZN Art. 3: deemed to have been published 1 January 1758].

1763

Scopoli, J.A. 1763. Entomologia Carniolica exhíbens insecta Carnioliae indigena et distributa in ordines, genera, species, varietates. Methodo Linnaeana. Ioannis Thomae Trattner, Vindobonae [Vienna]. Pp. 38 unnumbered + 1–419 + 680 figs. [43 unnumbered plates].

1767

Linnaeus, C. 1767. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis locis. Editio duodecima reformata. Tomus 1, pars 2. Stockholm Laurentius Salvius, Stockholm. Pp. 533–1327 + [37].

1772

Pallas, P.S. 1772. Phalangia, Araneae, Acari. *In* Spicilegia Zoologica. Continens quadrupedium, avium, amphibiorum, piscium, insectorum, molluscorum aliorumque marinorum. Volume 1, Fascicle 9. Gott. August. Lange, Berolini [Berlin]. Pp. 28–50.

1775

Fabricius, J.C. 1775. *Systema Entomologiae, Sistens Insectorum Classes, Ordines, Genera, Species, adiectis Synonymis, Locis, Descriptionibus, Observationibus.* Officina Libraria Kortii, Flensburgi et Lipsiae [Flensburg and Leipzig, Germany]. Pp. xxxii + 1–832.

1776

Müller, O.F. 1776. Zoologiae Danicae Prodromus, seu Animalium Daniæ et Norvegiæ Indigenarum characteres, nomina, et synonyma imprimis popularium. Heineck & Faber [printed by Hallager], Havniae [Copenhagen]. Pp. xxxii + 1–274.

1778

Geer, C. de 1778. *In* Mémoires pour servir à l'histoire des insectes. Tome 7. Pierre Hesselberg, Stockholm. Pp. xii + 950, 49 pl.

1779

Fabricius, J.C. 1779. Reise nach Norwegen mit Bemerkungen aus der Naturhistorie und Oekonomie. C.E. Bohn, Hamburg. Pp. lxiv + 388 + [12].

1781

Fabricius, J.C. 1781. Species insectorum exhibentes eorum differentias specificas, synonyma auctorum, loca natalia, metamorphosin adiectis observationibus, descriptionibus. C.E. Bohn, Hamburgi et Kilonii [Hamburg and Kiel, Germany]. Tome 1, Pp. 1–552.

1792

Bosc, L.A.G. 1792. Description d'un *phalangium* et d'un *cinips*. Bulletin des Sciences, par la Société philomathique de Paris, 1 [de Juillet 1791, à Ventôse, an 7 (=1799)], 18. [Issued February 1792].

Olivier, G.A. 1792. Faucheur [encyclopedia article]. *In* Encyclopédie Méthodique. Tome 6 ["1791"], Histoire naturelle. Insectes. (D. Diderot & J. le R. D'Alembert, eds.). Charles Joseph Panckoucke (for the Société de Gens de Lettres, de Savans et d'Artistes), Paris. Pp. 455–461.

1793

Fabricius, J.C. 1793. Entomologia systematica emendata et aucta. Secundum classes, ordines, genera, species adjectis synonimis, locis, observationibus, descriptionibus. Tome 2. Christ. Gottl. Proft, Hafniae [Copenhagen]. Pp. viii + 1–519.

1794

Panzer, G.W.F. 1794. Faunae Insectorum Germanicae initia oder Deutschlands Insecten. Zweyter Jahrgang. XIII–XXIV Heft. Felseckersche Buchhandlung, Nürnberg. Pp. 1–284 + 284 pl.

Table 1.—Continued.

1795

Cuvier, G. 1795. Description de deux espèces nouvelles d'Insectes. Le Faucheux a 4–dentelures. Magazin Encyclopédique, N.S., Tome 1. Pp. 205–207 + pl. 2.

1796

Latreille, P.A. 1796. Précis des caractères génériques des insectes, disposés dans un ordre naturel. Prévot, Bourdeaux, Brive, Paris. Pp. XII + 202 + VI, 1 table.

1798

Herbst, J.F.W. 1798. Naturgeschichte der Insecten-Gattung *Opilio*. *In* Natursystem der ungeflügelten Insekten, Volume 2 [of 4]. (J.F.W. Herbst, ed.). G.A. Lange, Berlin. Pp. iv + 1–26 pp., 5 pl.

Latreille, P.A. 1798 Mémoire pour servir de suite à l'histoire des insectes connus sous le nom de Faucheurs. *Phalangium*. L. Bulletin des Sciences par la Société Philomathique, Paris. Volume 1(15), Pp. 113–115. [issue title pages: Prairial, an 6 (French Revolutionary Calendar) = June 1798].

1799

Herbst, J.F.W. 1799. Fortsetzung der Naturgeschichte der Insectengattung *Opilio*. *In* Herbst, J.F.W., Natursystem der ungeflügelten Insekten, Volume 3 [of 4]. (J.F.W. Herbst, ed.). G.A. Lange, Berlin. Pp. iv + 1–30, pl. 6–10.

1802

Latreille, P.A. 1802a. Histoire naturelle des fourmis, et recueil de mémoires et d'observations sur les abeilles, les araignées, les faucheurs, et autres insectes. Crapelet, Paris. Pp. xvi + 1–445, 12 pl. [Issued before 21 September 1802]

Latreille, P.A. 1802b. Famille Troisième. Phalangiens. *In* Histoire naturelle, générale et particulière des Crustacés et des Insectes. Volume 3. (C.S. Sonnini, ed.). F. Dufart, Paris. Pp. 60–62. [Issued 6 November 1802].

1804

Hermann, J.F. 1804. Mémoire aptérologique. Published posthumously by Fréderic-Louis Hammer. F.G. Levrault, Strassburg. Pp. viii + 1–144, 9 pl.

Latreille, P.A. 1804. Huitième genre-Dixième genre *In* Histoire naturelle, générale et particulière des Crustacés et des Insectes. Volume 7. (C.S. Sonnini, ed.). F. Dufart, Paris. Pp. 314–329.

In the first 30 years following the launch of modern taxonomy, an average of one species was described each four to five years. In the early 1790s this rate increased to one species each year, and nearing the close of the century six to seven new species were recorded each year.

It is important to note that the generic names *Phalangium* and *Opilio* were not separate entities then, but conflicting usages of the same genus. Herbst (1798, 1799) used the latter as a replacement for the former because he considered that the former was likely to cause confusion due to a long history of usage of *Phalangium* for spiders as well as any other arachnid considered "fearsome." All other authors followed Linnaeus using *Phalangium*. The use of *Phalangium* and *Opilio* as separate genera came only decades later with Koch (1848). Another usage strongly contrasting with the modern one is the treatment of *P. parietinum* and *P. opilio* as conspecific (which would only be universally disclaimed almost a century later) while using *P. cornutum* for what today we know as *P. opilio*.

Thus, all Opiliones were at one point in *Phalangium*, with the exceptions of a member of Dyspnoi, described in *Acarus* (Scopoli 1763) and the new genera *Trogulus* and *Siro*, erected

Table 2.—Nomenclatural acts regarding Opiliones from 1758 to 1804. The non-Opiliones originally included in *Phalangium* are only treated marginally.

Organism name	Author/year	Controlled term	Modifier	Sp. descry.	Synonym sp.	Revalidated sp.	Invalid sp.	Sp. diff.	Sp. cumulative
Phalangium	Linnaeus 1758	Gen. nov.	Of order Aptera, Type species *Phalangium opilio*, p. 618	0	0	0	0		
Phalangium opilio	Linnaeus 1758	Sp. nov.	Europa, America, p. 618	1	0	0	0	1	1
Phalangium caudatum	Linnaeus 1758	Sp. nov.	India, p. 619	1	0	0	1	0	1
Phalangium reniforme	Linnaeus 1758	Sp. nov.	America, p. 619	1	0	0	1	0	1
Acarus nepaeformis	Scopoli 1763	Sp. nov.	Carniola [Slovenia], p. 390	1	0	0	0	1	2
Phalangium cornutum	Linnaeus 1767	Sp. nov.	Germany, p. 1028	1	0	0	0	1	3
Phalangium tricarinatum	Linnaeus 1767	Sp. nov.	Germany, p. 1029	1	0	0	0	1	4
Phalangium acaroides	Linnaeus 1767	Sp. nov.	Tropical America, p. 1028	1	0	0	1	0	4
Phalangium grossipes	Linnaeus 1767	Sp. nov.	Norwegian Sea, p. 1027	1	0	0	1	0	4
Phalangium balaenarum	Linnaeus 1767	Sp. nov.	p. 1028	1	0	0	1	0	4
Phalangium cancroides	(Linnaeus 1758)	Comb. nov.	Transferred from *Acarus*, p. 1028	0	0	0	0	0	4
Acarus cancroides	Linnaeus 1758	Referred to	*Phalangium*, p. 1028	0	0	0	0	0	4
Phalangium lunatum	Pallas 1772	Sp. nov.	South America, p. 35, pl. 3, figs. 5, 6	1	0	0	1	0	4
Phalangium araneoides	Pallas 1772	Sp. nov.	Russia, p. 37, pl. 3, figs. 7–9	1	0	0	1	0	4
Phalangium bimaculatum	Fabricius 1775	Sp. nov.	England, p. 440	1	0	0	0	1	5
Phalangium lugubre	Müller 1776	Sp. nov.	Denmark and/or Norway, p. 192	1	0	0	0	1	6
Phalangium mucronatum	Müller 1776	Sp. nov.	Denmark and/or Norway, p. 192	1	0	0	1	0	6
Phalangium parietinum	De Geer 1778	Sp. nov.	[Sweden], p. 166, pl. 10, figs. 1–11	1	0	0	0	1	7
Phalangium opilio	Linnaeus 1758	Syn. Nov.	*Phalangium parietinum* De Geer 1778	0	0	0	0	0	7
Phalangium parietinum	De Geer 1778	New synonym	Of *Phalangium opilio* Linnaeus 1758, p. 459	0	1	0	0	−1	6
Phalangium bimaculatum	Fabricius 1775	Syn. nov.	*Phalangium lugubre* Müller 1776	0	0	0	0	0	6
Phalangium lugubre	Müller 1776	New synonym	Of *Phalangium bimaculatum* Fabricius 1775, p. 440	0	1	0	0	−1	5
Phalangium coronatum	Fabricius 1779	Sp. nov.	Norway, p. 339	1	0	0	0	1	6
Phalangium diadema	Fabricius 1779	Sp. nov.	Norway, p. 339	1	0	0	0	1	7
Phalangium morio	Fabricius 1779	Sp. nov.	Norway, p. 340	1	0	0	0	1	8
Phalangium bilineatum	Fabricius 1779	Sp. nov.	p. 360	1	0	0	1	0	8
Phalangium cristatum	Olivier 1792	Sp. nov.	France, p. 460	1	0	0	1	0	8
Phalangium annulatum	Olivier 1792	Sp. nov.	Switzerland, p. 459	1	0	0	0	1	9
Phalangium carinatum	(Linnaeus 1767)	Subseq. incorr. spelling	for *Phalangium tricarinatum*, p. 460	0	0	0	0	0	9
Phalangium diadema	Fabricius 1779	Syn. nov.	*Phalangium coronatum* Fabricius 1779	0	0	0	0	0	9
Phalangium coronatum	Fabricius 1779	New synonym	Of *Phalangium diadema* Fabricius 1779, p. 339	0	1	0	0	−1	8
Phalangium spinosum	Bosc 1792	Sp. nov.	France, p. 18	1	0	0	0	1	9
Phalangium bicolor	Fabricius 1793	Sp. nov.	Switzerland, p. 429	1	0	0	0	1	10
Phalangium carinatum	(Linnaeus 1767)	Subseq. incorr. spelling	for *Phalangium tricarinatum*, p. 431	0	0	0	0	0	10
Phalangium hellwigii	Panzer 1794	Sp. nov.	Germany, p. 13, unnumb. pl.	1	0	0	0	1	11
Phalangium horridum	Panzer 1794	Sp. nov.	Germany, p. 21, unnumb. pl.	1	0	0	0	1	12
Phalangium 4-dentatum	Cuvier 1795	Sp. nov.	p. 206, pl. 2., fig. 4.	1	0	0	0	1	13
Phalangium cornutum	Linnaeus 1767	New synonym	Of *Phalangium opilio* Linnaeus 1758, p. 114	0	1	0	0	−1	12
Phalangium opilio	Linnaeus 1758	Syn. nov.	*Phalangium cornutum* Linnaeus 1767, p. 114	0	0	0	0	0	12
Phalangium histrix	Latreille 1798	Sp. nov.	Loc. not stated, p. 114	1	0	0	0	1	13
Phalangium palliatum	Latreille 1798	Sp. nov.	France, p. 114	1	0	0	0	1	14
Phalangium rostratum	Latreille 1798	Sp. nov.	Loc. not stated, p. 114	1	0	0	0	1	15
Phalangium rotundum	Latreille 1798	Sp. nov.	[France], p. 115	1	0	0	0	1	16

Table 2.—Continued.

Organism name	Author/year	Controlled term	Modifier	Sp. descry.	Synonym sp.	Revalidated sp.	Invalid sp.	Sp. diff.	Sp. cumulative
Phalangium muscorum	Latreille 1798	Sp. nov.	[France], p. 114	1	0	0	1	0	16
Opilio parietinus	(De Geer 1778)	Comb. nov.	Transferred from *Phalangium*, p. 12	0	0	0	0	0	16
Phalangium parietinum	De Geer 1778	Referred to	*Opilio*, p. 12	0	0	0	0	0	16
Opilio cornutus	(Linnaeus 1767)	Comb. nov.	Transferred from *Phalangium*, p. 13	0	0	0	0	0	16
Phalangium cornutum	Linnaeus 1767	Removal from synonymy; referred to	With *Phalangium opilio*, p. 13; *Opilio*, p. 13	0	0	1	0	1	17
Opilio bicolor	(Fabricius 1793)	Comb. nov.	Transferred from *Phalangium*, p. 15	0	0	0	0	0	17
Phalangium bicolor	Fabricius 1793	Referred to	*Opilio*, p. 15	0	0	0	0	0	17
Opilio morio	(Fabricius 1779)	Comb. nov.	Transferred from *Phalangium*, p. 16	0	0	0	0	0	17
Phalangium morio	Fabricius 1779	Referred to	*Opilio*, p. 16	0	0	0	0	0	17
Opilio Helwigii	(Panzer 1794)	Comb. nov.	Transferred from *Phalangium*, p. 16	0	0	0	0	0	17
Phalangium hellwigii	Panzer 1794	Referred to	*Opilio*, p. 16	0	0	0	0	0	17
Opilio diadema	(Fabricius 1779)	Comb. nov.	Transferred from *Phalangium*, p. 25	0	0	0	0	0	17
Phalangium diadema	Fabricius 1779	Referred to	*Opilio*, p. 25	0	0	0	0	0	17
Opilio horridus	(Panzer 1794)	Comb. nov.	Transferred from *Phalangium*, p. 7	0	0	0	0	0	17
Phalangium horridum	Panzer 1794	Referred to	*Opilio*, p. 7	0	0	0	0	0	17
Opilio 4dentatus	(Cuvier 1795)	Comb. nov.	Transferred from *Phalangium*, p. 13	0	0	0	0	0	17
Phalangium 4-dentatum	Cuvier 1795	Referred to	*Opilio*, p. 13	0	0	0	0	0	17
Opilio carinatus	(Linnaeus 1767)	Comb nov; subseq. incorr. spelling	Transferred from *Phalangium*, p. 13; for *Phalangium tricarinatum*	0	0	0	0	0	17
Phalangium tricarinatum	Linnaeus 1767	Referred to	*Opilio*, p. 13	0	0	0	0	0	17
Opilio fasciatus	Herbst 1798	Sp. nov.	Germany, p. 23, pl. 4, figs. 1, 2.	1	0	0	0	1	18
Opilio hispidus	Herbst 1798	Sp. nov.	Germany, p. 20, pl. 3, figs. 1, 2.	1	0	0	0	1	19
Opilio longipes	Herbst 1798	Sp. nov.	Germany, p. 22, pl. 2, fig. 2.	1	0	0	0	1	20
Opilio monocanta	Herbst 1798	Sp. nov.	SE Asia, p. 19, pl. 2, fig. 1.	1	0	0	1	0	20
Opilio alpinus	Herbst 1799	Sp. nov.	France, p. 3, pl. 6, fig. 2.	1	0	0	0	1	21
Opilio grossipes	Herbst 1799	Sp. nov.	Germany, p. 1, pl. 6, fig. 1.	1	0	0	0	1	22
Opilio hemisphaericus	Herbst 1799	Sp. nov.	Germany, p. 11, pl. 9, fig. 2.	1	0	0	0	1	23
Opilio palpinalis	Herbst 1799	Sp. nov.	[Germany], p. 6, pl. 7, fig. 2.	1	0	0	0	1	24
Opilio rupestris	Herbst 1799	Sp. nov.	Germany, p. 4, pl. 7, fig. 1.	1	0	0	0	1	25
Opilio scaber	Herbst 1799	Sp. nov.	"Hungary" [now Romania], p. 15, pl. 8, fig. 2.	1	0	0	0	1	26
Opilio spinosus	Herbst 1799	Sp. nov.	Germany, p. 8, pl. 9, fig. 1.	1	0	0	0	1	27
Opilio triangularis	Herbst 1799	Sp. nov.	Germany, p. 9, pl. 10, fig. 2.	1	0	0	0	1	28
Phalangita	Latreille 1802	Fam. nov.	fam. n., Phalangita [Insecta Acera], p. 60	0	0	0	0	0	28
Trogulus	Latreille 1802	Gen. nov.	Of family Phalangita, type species not designated, p. 61	0	0	0	0	0	28
Siro	Latreille 1802	Gen. nov.	Of family Phalangita, type species *Siro rubens*, p. 62	0	0	0	0	0	28
Siro rubens	Latreille 1802	Sp. nov.	[France], p. 62	1	0	0	0	1	29
Trogulus nepaeformis	(Scopoli 1763)	Comb. nov.	Transferred from *Acarus* p. 61	0	0	0	0	0	29
Acarus nepaeformis	Scopoli 1763	Referred to	*Trogulus*, p. 61	0	0	0	0	0	29
Trogulus rostratus	(Latreille 1798)	Comb. nov.	Transferred from *Phalangium*, p. 61	0	0	0	0	0	29
Phalangium rostratum	Latreille 1798	Referred to	*Trogulus*, p. 61	0	0	0	0	0	29
Phalangium rostratum	Latreille 1798	New synonym	Of *Acarus nepeformis* Scopoli 1763, p. 328	0	1	0	0	−1	28
Acarus nepeformis	Scopoli 1763	Syn. nov.	*Phalangium rostratum* Latreille 1798	0	0	0	0	0	28
Phalangium tricarinatum	Linnaeus 1767	New synonym	Of *Acarus nepeformis* Scopoli 1763, p. 327	0	1	0	0	−1	27

Table 2.—Continued.

Organism name	Author/year	Controlled term	Modifier	Sp. descry.	Synonym sp.	Revalidated sp.	Invalid sp.	Sp. diff.	Sp. cumulative
Acarus nepeformis	Scopoli 1763	Syn. nov.	*Phalangium tricarinatum* Linnaeus 1767, p. 327	0	0	0	0	0	27
Phalangium chrysomelas	Hermann 1804	Sp. nov.	[France], p. 108, pl. 8, fig. 3	1	0	0	0	1	28
Phalangium cornigerum	Hermann 1804	Sp. nov.	[France], p. 102, pl. 8, figs. 2E–G	1	0	0	0	1	29
Phalangium melanotarsum	Hermann 1804	Sp. nov.	[France], p. 103, pl. 5, fig. 2.	1	0	0	0	1	30
Phalangium rufum	Hermann 1804	Sp. nov.	[France], p. 109, pl. 8., fig. 1	1	0	0	0	1	31
Phalangium spinulosum	Hermann 1804	Sp. nov.	[France], p. 107, pl. 7, fig. 1	1	0	0	0	1	32
Phalangium urnigerum	Hammer in Hermann 1804	Sp. nov.	France, p. 110, pl. 9, figs. 2, 3	1	0	0	0	1	33
Phalangium rubens	Hermann 1804	Sp. nov.	[France], p. 105	1	0	0	1	0	33
Phalangium uncatum	Hermann 1804	Sp. nov.	[France], p. 106, pl. 8, fig. 5	1	0	0	1	0	33

by Latreille (1802b) at the end of the period considered here. A possible checklist of the Opiliones of the world as it would have been in 1804 is shown in Table 3, with the species described by Herbst included in *Phalangium* as opposed to *Opilio*. The species inquirendae have not been included. There is more than one possible checklist, depending on which of the synonymies to accept in the triangle involving *P. opilio*, *P. cornutum*, and *P. parietinum*, which could be mutually exclusive or not. Also, one could interpret differently the creation of the name *Opilio*, either as a junior synonym of *Phalangium* or as an unjustified replacement name.

STEP-BY-STEP HISTORICAL ACCOUNT

Carolus Linnaeus (1758) defined a Classis V – Insecta (p. 339) containing among others the order 7 – Aptera (summary on p. 341 and complete description of species beginning on p. 608). He created (p. 618) the new genus #236 – *Phalangium*, containing three species of which only the first, *Phalangium Opilio* (p. 618), is presently regarded as a member of the Opiliones. *Phalangium Opilio* is thus the first of the Opiliones to be described and the first species of what today is known as Eupnoi. The other two species are today in Thelyphonida (*Phalangium caudatum*) and Amblypygi (*Phalangium reniforme*, a name suppressed by the ICZN).

The Italian-speaking Tyrolean (Austrian) physician and naturalist Giovanni Antonio Scopoli (1763) presented a work in Latin on the "insects" of Carniola (then part of Austria, and roughly corresponding to modern Slovenia), keeping the order Aptera of Linnaeus, but calling it Pedestria – Aptera (page 378). On p. 387, he started to list the species of the genus *Acarus*, from # 1056 to 1076. On page 390, he describes a new species # 1070, *Acarus Nepeformis*. This species is the first member of the present-day Dyspnoi to be described. The specific name appears written in two different spellings: *Nepæformis* (which would be the correct grammatical form) in the index and *Nepeformis* in the species heading. On p. 404, he cites *P. Opilio* (#1121) as the single species of the genus occurring in Carniola.

In the 12th edition of the Systema Naturae, Carolus Linnaeus (1767) once again treated the "Insecta Aptera" (starting on p. 1012). He listed the genus *Acarus* (starting on p. 1022) with 35 species, but overlooking Scopoli's species. He also listed his genus *Phalangium* now with nine other species, only three of which are Opiliones (the others include even marine arthropods), introducing two new species: *Phalangium cornutum* (on p. 1028 which is universally regarded today as the male of his own *Phalangium opilio*) and *Phalangium tricarinatum* (on p. 1029, the second species of today's Dyspnoi, which later would be included in *Trogulus* Latreille 1802). Among the six non-Opiliones species are *Phalangium cancroides* (transferred by Linnaeus from *Acarus*) and *Phalangium Acaroides* (new name, seemingly intended as a replacement for *Acarus scorpioides* Linnaeus 1758), both currently in Pseudoscorpiones; *Phalangium grossipes* and *Phalangium Balaenarum* (currently in Pycnogonida), and the two species of Amblypygi and Thelyphonida cited in 1758.

The German zoologist Peter Pallas published in his finely illustrated *Spicilegia Zoologica* a section on *Phalangium* (1772), but added no genuine Opiliones. He redescribed and illustrated the Linnean Amblypygi and Thelyphonida de-

Table 3.—Checklist of the valid species in the order Opiliones up to 1804. The species later proved extraneous to the Opiliones and the unrecognizable species are not included. The current suborders of Opiliones are included for familiarity. Some of the combinations of Herbst's *Opilio* species under *Phalangium* did not exist in 1804 and are included here as if done by a fictional author who prepared a checklist with the then available knowledge. The decision to consider *Opilio* as a genus separate from *Phalangium* was taken only much later.

Species name as if used in 1804	Current combination and/or synonymy
Cyphophthalmi	
Siro rubens Latreille, 1802	*Siro rubens* Latreille 1802
Dyspnoi	
Phalangium bimaculatum Fabricius, 1775 (= *Phalangium lugubre* Müller 1776)	*Nemastoma bimaculatum* (Fabricius, 1775)
Phalangium chrysomelas Hermann, 1804	*Mitostoma chrysomelas chrysomelas* (Hermann, 1804)
Phalangium hellwigii Panzer, 1794	*Ischyropsalis hellwigii hellwigii* Panzer, 1794
Phalangium melanotarsum Hermann, 1804	Junior synonym of *Trogulus nepaeformis* (Scopoli, 1763)
Phalangium scabrum (Herbst, 1799)	*Dicranolasma scabrum* (Herbst, 1799)
Trogulus nepaeformis (Scopoli, 1763) (= *Phalangium tricarinatum* Linnaeus, 1767; = *Phalangium rostratum* Latreille, 1798)	*Trogulus nepaeformis* (Scopoli, 1763)
Eupnoi	
Phalangium alpinum (Herbst, 1799)	Junior synonym of *Mitopus morio* (Fabricius 1779)
Phalangium annulatum Olivier, 1792	*Gyas annulatus* (Olivier, 1792)
Phalangium bicolor Fabricius, 1793	Junior synonym of *Gyas annulatus* (Olivier, 1792)
Phalangium cornigerum Hermann, 1804	Junior synonym of *Rilaena triangularis* (Herbst 1799)
Phalangium diadema Fabricius, 1779 (= *Phalangium coronatum* Fabricius, 1779)	*Megabunus diadema* (Fabricius 1779)
Phalangium fasciatum (Herbst, 1798)	Junior synonym of *Leiobunum rotundum* (Latreille, 1798)
Phalangium grossipes (Herbst, 1799)	Junior synonym of *Mitopus morio* (Fabricius 1779)
Phalangium hemisphaericum (Herbst, 1799)	Junior synonym of *Leiobunum rotundum* (Latreille, 1798)
Phalangium hispidum (Herbst, 1798)	Junior synonym of *Lacinius horridus* (Panzer 1794)
Phalangium histrix Latreille, 1798	Junior synonym of *Odiellus spinosus* (Bosc, 1792)
Phalangium horridum Panzer, 1794	*Lacinius horridus* (Panzer 1794)
Phalangium longipes (Herbst, 1799)	Junior synonym of *Opilio parietinus* (de Geer 1778)
Phalangium morio Fabricius, 1779	*Mitopus morio* (Fabricius 1779)
Phalangium opilio Linnaeus, 1758 (= *Phalangium cornutum* Linnaeus, 1767)	*Phalangium opilio* Linnaeus, 1758
Phalangium palliatum Latreille, 1798	Junior synonym of *Mitopus morio* (Fabricius 1779)
Phalangium palpinale (Herbst, 1799)	*Lophopilio palpinalis* (Herbst 1799)
Phalangium parietinum de Geer, 1778 (revalidated)	*Opilio parietinus* (de Geer 1778)
Phalangium quadridentatum Cuvier, 1795	*Homalenotus quadridentatus* (Cuvier 1795)
Phalangium rotundum Latreille, 1798	*Leiobunum rotundum* (Latreille, 1798)
Phalangium rufum Hermann, 1804	Junior synonym of *Opilio parietinus* (de Geer 1778)
Phalangium rupestre (Herbst, 1799)	*Leiobunum rupestre* (Herbst 1799)
Phalangium spinosum Bosc, 1792	*Odiellus spinosus* (Bosc, 1792)
Phalangium spinosum (Herbst, 1799) [junior secondary homonym of *Phalangium spinosum* Bosc, 1792]	*Astrobunus spinosus* (Herbst 1799)
Phalangium spinulosum Hermann, 1804	Junior synonym of *Lophopilio palpinalis* (Herbst 1799)
Phalangium triangulare (Herbst, 1799)	*Rilaena triangularis* (Herbst 1799)
Phalangium urnigerum Hammer in Hermann, 1804	Junior synonym of *Mitopus morio* (Fabricius 1779)

scribed under *Phalangium* and described two species of his own: *P. lunatum* (currently *Phrynichus lunatus* – Amblypygi), and *P. araneoides* (Solifugae). The type locality of *P. araneoides* is often quoted as from South Africa because of the observation by Pallas that he judged the species illustrated by botanist Johannes Burmann in "picturas Capenses" the same as his. Pallas's detailed description is based on presumably Russian material in the Saint Petersburg Museum.

The Danish entomologist Johann Christian Fabricius (1775) divided the "insects" into eight classes, of which the fifth was Unogata, including genera today grouped in Odonata, Diplopoda, Chilopoda, Acari, Araneae, and Opiliones. He (Fabricius 1775:440–441) cited six species of his genus # 137, *Phalangium* (of which three are not Opiliones: *P. grossipes*, *P. reniforme*, *P. caudatum*), including *P. opilio*, *P. cornutum*, and describing from England the new species *Phalangium bimaculatum*, the first of the future genus *Nemastoma* C.L. Koch 1836, which would be described only 60 years later. He ignored *Phalangium tricarinatum*.

The Danish naturalist Otto Müller (1776) published a list of the fauna of Denmark and Norway, which were then united in a single country called Denmark–Norway (including Iceland, Greenland, and the Faroe Islands). On pp. 191–192, he listed the genus *Phalangium* with nine species, of which many are unrecognizable (four Linnean extraneous species + *P. mucronatum* and two species without a binomen, # 2298 and 2299). He included # 2292 – *Phalangium opilio* and the new species # 2297 – *Phalangium lugubre*, which is the fourth described species now placed in Dyspnoi, and the second that would later become *Nemastoma*.

The Swedish entomologist, Baron Charles de Geer (also spelled De Geer and DeGeer) published the seventh tome of

Table 4.—Species described in *Opilio*/*Phalangium* but which are either not Opiliones or are unrecognizable (nomina dubia). 14 species have been originally described as new *Opilio*/*Phalangium* and 1 has been transferred from *Acarus*.

Species name	Author/Year	Status
Phalangium acaroides	Linnaeus, 1767	Pseudoscorpiones
Phalangium araneoides	Pallas, 1772	Solifugae
Phalangium balaenarum	Linnaeus, 1767	Pycnogonida
Phalangium bilineatum	Fabricius, 1779	Opiliones - unrecognizable
Phalangium cancroides	(Linnaeus, 1758)	Pseudoscorpiones
Phalangium caudatum	Linnaeus, 1758	Thelyphonida
Phalangium cristatum	Olivier, 1792	Opiliones - unrecognizable
Phalangium grossipes	Linnaeus, 1767	Pycnogonida
Phalangium lunatum	Pallas,1772	Amblypygi
Opilio monocanta	Herbst 1798	Opiliones - unrecognizable
Phalangium mucronatum	Müller, 1776	Opiliones - unrecognizable
Phalangium muscorum	Latreille, 1798	Opiliones - unrecognizable
Phalangium reniforme	Linnaeus, 1758	Amblypygi
Phalangium rubens	Hermann, 1804	Opiliones - unrecognizable
Phalangium uncatum	Hermann, 1804	Opiliones - unrecognizable

an entomological compendium (1778) written in French, treating many "Insecta Aptera." In his Treizième Classe (which included the Arachnida and some Crustacea), he listed the genus *Phalangium* as the family 89 – *Le Faucheur*' He mentioned and illustrated only two species of *Phalangium*, the first, which he called *Faucheur des murailles* (which translates as "harvestman of the walls," while Latin *parietinus* also means "of the walls"), bearing the new binomen *Phalangium parietinum* (p. 166). It would much later become the type of *Opilio* Herbst 1798. Also, he featured as a synonym Linnaeus's *Phalangium Opilio*. De Geer did not explain why he considered his name as valid over the original, which had 20 years of precedence. He was the first of many authors to consider *Phalangium Opilio* as a synonym of *Phalangium parietinum* and to call "*P. cornutum*" the species that is today known as *Phalangium opilio*. On p. 173, he listed Linnaeus's *Phalangium cornutum*, remarking that this species is rare in Sweden, but abundant in the Netherlands and Germany. Notably, de Geer was the first author who did not lump other arachnid orders together with harvestmen in the genus; his use of the word *Faucheur* implies that he considered *Phalangium* to consist only of Opiliones.

Fabricius (1779:330) considered Müller's *Phalangium lugubre* as a synonym of his own *Phalangium bimaculatum*, a synonymy that was widely accepted for two centuries, until Gruber & Martens (1968) validated both species. He also described three new Norwegian species, *Phalangium morio* which would later become the type of *Mitopus* Thorell 1876, *Phalangium Diadema* (today placed in *Megabunus* Meade 1855), and *Phalangium bilineatum* (nomen dubium). He provided the name *Phalangium coronatum* for one of Müller's non-binominal species; this also was later considered a nomen dubium. A little later, Fabricius (1781) gave a synopsis of *Phalangium* (his genus # 139), listing ten valid species (of which five are not opilionids, basically the other arachnids of Linnaeus and Pallas). In his species # 2, he followed the synonymy proposed by de Geer, differing in the recognition of the correct order of precedence, that is, *Phalangium parietinum* as a junior synonym to *Phalangium opilio*.

The Frenchman Guillaume Olivier published an article about harvestmen in the *Encyclopédie Méthodique* (Olivier 1792). He was the first to remove from *Phalangium* the species *caudatum*, *reniforme*, and *lunatum*, to place them in the new genus *Phrynus* (though strangely, the authority on this is often given as Lamarck 1801) and transferred *P. aranoides* to *Galeodes*. He listed a total of nine species in *Phalangium*, all of which are Opiliones. He described one new species, 1. 'Faucheur annulaire' = *Phalangium annulatum*, from Switzerland (which would later become the type of *Gyas* Simon 1879), recognized both Norwegian species described by Fabricius (1779), 2. 'Faucheur morio' and 6. 'Faucheur diadème' (listing *Phalangium coronatum* Fabricius as a synonym, an act ignored by later authors), followed the precedence adopted by Fabricius (1781) (i.e., *Phalangium parietinum* as junior to 3. 'Faucheur des murailles' = *Phalangium opilio*.) He listed also Linnaeus' 4. 'Faucheur cornu' = *Phalangium cornutum*; 8. 'Faucheur carené' = *Phalangium carinatum*, which is only a new name (unjustified emendation) for Linnaeus's *Phalangium tricarinatum*; and 9. 'Faucheur bimaculé' = *Phalangium bimaculatum* Fabricius. In his list, there are finally 5. 'Faucheur bilinée' = *Phalangium bilineatum* Fabricius (today a species inquirenda) from Norway and added a new species from Paris, 7. 'Faucheur en-crête' = *Phalangium cristatum*, which is also a species inquirenda.

In France, Louis Bosc (1792) described, without mentioning other species, a *Phalangium spinosum*, from around Paris, which today is the type of *Odiellus* Roewer 1923.

Fabricius (1793) recognized nine species of *Phalangium*, among them the Russian solpugid *Phalangium araneoides* Pallas, already removed to *Galeodes* by Olivier, and the nomen dubium *P. bilineatum*. Of the seven remnant species, he described one as new, *Phalangium bicolor* from Switzerland (later synonymized with Olivier's species *Phalangium annulatum*) and listed the three species of Linnaeus (keeping Olivier's unjustified emendation *carinatum*) and the two Norwegian species described earlier by himself (but spelling *bimaculatum* as *2maculatum*). Fabricius proposed a synonymy of an African solpugid with *Phalangium araneoides*. It seems that Fabricius was following Pallas in accepting an extremely wide species concept and distribution, producing an even less probable synonymy. A few years later, Fabricius (1798) cited the more accepted type locality for *Phalangium araneoides* as "Habitat in Russia australi."

The German Georg Panzer did not mention any other *Phalangium* when he described the new species *Phalangium Hellwigii*, from Germany (1794, 8:13), today placed in *Ischyropsalis* C.L. Koch 1839; and *Phalangium horridum* (1794, 17:21), today in *Lacinius* Thorell 1876. Cuvier (1795) described the new species *Phalangium 4-dentatum* from France. Later this species was made the type of *Homalenotus* C.L.Koch 1839. The great French zoologist Pierre Latreille published (1796) the new genus *Siro*, without any included species, failing thus to comply with ICZN art. 12.2.5.; therefore *Siro* Latreille 1796 is an unavailable name, the first species indicated being described only in 1802 (see below).

The work of the German entomologist Johann Herbst (1798–1799) brought a major change. Herbst (1798:1) presented the state of the art for the genus *Phalangium*, created the new generic name *Opilio* to be used as a replacement for *Phalangium* and provided a long-winded explanation for doing so. Basically, he regarded the genus *Phalangium* as too heterogeneous and perhaps also the usage (*Phalangium* is a Latin word used by the Roman naturalist Pliny and many other pre-Linnean authors for spiders regarded as "venomous") very unfortunate. Rod Crawford (pers. comm.) noted: "Practically every author before Linnaeus had used that name for actual spiders that were considered dangerously venomous. Linnaeus, primarily a botanist, ignored previous usage, much to Herbst's annoyance. Herbst had a very similar problem with the Fabricius amblypygid genus *Tarantula* (which most people in his day knew as the vernacular name of a wolf spider)." This could be regarded as an unjustified nomen novum. Contemporary authors ignored the name *Opilio* and continued to use *Phalangium*. Only much later was *Opilio* revived by Koch (1848). Simon (1879), in spite of regarding *Opilio* as a junior synonym of *Phalangium*, explicitly fixed *Phalangium parietinum* as the type species of *Opilio*, as noted by Crawford (1992). Herbst provided a list of the species of *Opilio* with 23 (12 + 11) species, long diagnoses, and profusely illustrated color plates. Among the contents may be cited: 1) the defense of de Geer's precedence of *P. parietinum* vs. *P. opilio* against Fabricius and Olivier; 2) the description of the first tropical harvestman, *O. monocanta* (spelled *monocantha* on plate) from "Ostindien" [SE Asia] — this species obviously belongs in Gagrellinae as stated by Roewer (1923:1088), but Herbst's description is insufficient to determine the species, and it should be listed as species inquirenda; 3) description of nine new species from Germany, one from Hungary (*Opilio scaber*, nominally as from historical Hungary, now Romania) and one from France. 180 years later, Martens (1978:156) concluded that *Opilio scaber* came from the Carpathian region, restricting the locus typicus to Sibiu, Romania. Herbst's list is fairly complete, omitting the two synonymized species *P. opilio* and *P. lugubre*, the two species described by Bosc and Olivier in 1792, *P. annulatum* and *P. spinosum* and, as all previous authors did, *Acarus nepæformis* and the genus *Siro*, which were not then recognized as opilionids.

Simultaneously with the work of Herbst, Pierre Latreille published a synopsis of the Opiliones (Latreille 1798), so that the two works do not mention each other. Latreille cites 10 species of *Phalangium*, of which five were new: *Phalangium rotundum*, which later became the type of *Leiobunum*; *P. histrix*, today in *Odiellus*; *P. palliatum* (a synonym of *P. morio*); *P. muscorum*; unidentifiable and *P. rostratum*; which later was transferred to *Trogulus*. He appears to have explicitly chosen a new alternative name to an existing species, *P. spinosum* for Cuvier's *P. quadridentatum*, probably because he regarded the name as inadequate. He is the first to notice that *P. cornutum* and *P. opilio* are the male and female, respectively, of the same species; he correctly gave *P. opilio* priority, but did not mention *P. parietinum*, which he presumably considered a synonym.

Within a few months Latreille published two works on Opiliones, the first (1802a) repeating his 1798 paper, with a list of the *Phalangium* occurring in France, and the other (1802b) with an outline of the four genera of his new family Phalangita, considerably expanding the group with the addition of the new genera *Trogulus* (for the first time bringing *Acarus nepæformis* Scopoli 1763 into Opiliones together with his own *Phalangium rostratum* Latreille 1798) and *Siro* (the first formal description of a cyphophthalm species, *Siro rubens*, making the genus *Siro* available). Also included was one non-harvestman, the solpugid *Galeodes* Olivier. In this paper, typified names of families are introduced between Linnaean orders and genera, being a very early example of this usage. This paper also marks the fixation of the spelling of the name *nepæformis* vs. *nepeformis*, by the principle of the first reviser. ICZN Art. 24.2.3. mandates that the first reviser must "have cited them **together** and to have **selected** one spelling as correct"; however, Latreille's choice has been universally followed and for the sake of stability, it is here recognized as a fixation of correct spelling.

In Buffon's Natural History, Latreille (1804) provided a list of 12 species of *Phalangium*, with some tentative synonymies. He uncharacteristically (although correctly) uses for the first time Cuvier's name *P. quadridentatum*, listing his own species *P. spinosum* as a junior synonym. He also equates, although tentatively, his *P. palliatum* with Fabricius' *P. morio*, *P. annulatum* Olivier 1792 = *P. bicolor* Fabricius 1793, *Opilio hispidus* Herbst 1798 = *P. horridum* Panzer 1794. When treating the genus *Trogulus*, he synonymized his own *Phalangium rostratum* and *Phalangium tricarinatum* Linnaeus (which he calls "carinatum" like many other authors) with *Acarus nepæformis* Scopoli 1763, which he chose to call neither *nepeformis* nor *nepæformis*, but a third spelling *nepiformis*, corresponding to the spelling of the modern sound of "nepæformis." In this work, Latreille (1804:329) also mentions the Cyphophthalmi. But his text is highly misleading, giving the impression that *Siro rubens* is a new species, although it had been properly described by himself two years before. Follows his text: "Je le nommerai ciron rougeâtre (siro rubens). Je ne crois pas qu'il ait été décrit." which translates as: "I will call it red mite (Siro rubens). I do not think it has been described." Perhaps this anomaly was due to Sonnini using a version Latreille had submitted to him years earlier.

The period considered here ends with the Mémoire Aptérologique of the deceased young Frenchman Jean-Fréderic Hermann (1804) posthumously published by Hammer. He heavily criticized the heterogeneous composition of *Phalangium* sensu Linnaeus and followed Olivier in removing all extraneous species, leaving only those corresponding to the vernacular name *faucheur*. He did not use Latreille's name

Phalangita, including *Phalangium* in the "family" Holetra. He considered *P. parietinum* to be a synonym of *P. opilio*, and *P. cornutum* a good species, like de Geer and Fabricius, *contra* Latreille. He described nine new species, including 1) *Phalangium cornigerum*, now under synonymy in *Rilaena*; 2) *Phalangium melanotarsum*, now under synonymy in *Trogulus*; 3) *P. rubens* (spelled like this in the description, p. 105, but as *Phalangium rubicundum* in the index, on p. 97) — this species is not the same as Latreille's *Siro rubens*, has never been cited again, and it is unrecognizable beyond clearly belonging to Eupnoi; 4) *Phalangium uncatum*, unrecognizable (immature); 5) *Phalangium spinulosum*, now under synonymy in *Lophopilio*; 6) *Phalangium chrysomelas*, today in *Mitostoma*; 7) *P. rufum*, now under synonymy in *Opilio*; 8) a *Phalangium annulatum*, based on scattered drawings and inserted as new by the editor, never cited again, which either is the same-named species by Olivier or a homonym; and 9) *P. urnigerum*, now under synonymy in *Mitopus*. "In the same publication Hermann described two species, *Acarus testudinarius* (pp. 80–82, Pl. IX, fig. 1) and *Acarus crassipes* (p. 80) that were erroneously interpreted by Lamarck (1838:95) as belonging to the genus *Siro*." (Giribet 2000).

Thus, at the beginning of the 19th century, what are today Eupnoi, Dyspnoi, and Cyphophthalmi, as well as what would later become the main European genera, had already been recognized, and there was a nucleus of 15–20 species of *Phalangium* universally recognized among the taxonomists. The non-Opiliones had already been purged from the list. The immediate post-Linnean generation of entomologists was gradually being replaced as its beacons died off: de Geer (1778), Müller (1784), Hermann (1794), Herbst (1807), Fabricius (1808), Pallas (1811), Olivier (1814), Bosc (1828), with only Latreille enduring another three decades. The order Opiliones had not yet received this name, and members from the tropics were virtually unknown. That, however, was about to change with the travels of the scientific French ships around the world (1817–1820) and the Brazilian expedition of Spix and von Martius (1817–1820).

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On the native Nearctic species of the huntsman spider family Sparassidae Bertkau (Araneae)

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Abstract. The native Nearctic species of the family Sparassidae are revised. Eight synonymies are proposed, reducing the number of species to five: *Olios schistus* Chamberlin 1919, *O. scepticus* Chamberlin 1924 and *O. positivus* Chamberlin 1924 with *O. peninsulanus* Banks 1898; *O. albinus* Fox 1937 and *O. foxi* Roewer 1951 with *O. naturalisticus* Chamberlin 1924. *Olios concolor* Keyserling 1884 and *O. pragmaticus* Chamberlin 1924 are removed from the synonymy of *O. fasciculatus* Simon 1880 and synonymized with *O. giganteus* Keyserling 1884. All species currently included in the genus *Olios* Walckenaer 1837 are redescribed and illustrated, and new distribution records are presented. Comparisons between these species and the type species of the genus *Olios*, *Olios argelasius* (Walckenaer 1805), shows that none of them are congeneric and that true *Olios* does not occur in the Nearctic region. Nevertheless, the correct placement of these species in new genera will only be possible after a more thorough revision of the Nearctic and Neotropical fauna, especially that of Mexico and Central America.

Keywords: *Olios giganteus*, *Olios bibranchiatus*, *Olios peninsulanus*, *Olios naturalisticus*, revision, synonymies, taxonomy

The Nearctic region comprises most of the North American continent, including Greenland and the northern highlands of Mexico (Udvardy 1975). To date, only thirteen Sparassidae species have been described from this region (eight from the USA and five from Northern Mexico), all assigned to the genus *Olios* Walckenaer 1837: *Olios franklinus* Walckenaer 1837, *O. concolor* Keyserling 1884, *O. giganteus* Keyserling 1884, *O. peninsulanus* Banks 1898, *O. schistus* Chamberlin 1919, *O. naturalisticus* Chamberlin 1924, *O. positivus* Chamberlin 1924, *O. scepticus* Chamberlin 1924, *O. pragmaticus* Chamberlin 1924, *O. albinus* Fox 1937, *O. bibranchiatus* Fox 1937, *O. mojavensis* Fox 1937 and *O. foxi* Roewer 1951 (Platnick 2010).

Olios franklinus, the first sparassid to be described from the Nearctic region, was proposed by Walckenaer (1837) from the USA. Nevertheless, the female type was never located and the identity of the species is considered doubtful.

Olios fasciculatus was described by Simon (1880), based on a male and female from Mariposa County, California, USA. Roth (1988) examined the type series and, based on Simon's description, designated a male lectotype. Nevertheless, no females fitting the original description were found amongst those in the type series suggesting that these were added posteriorly and were not conspecific with the described male. Also, since no other *Olios* specimens were found in the collections from California, Roth raised the possibility that the vial was actually mislabeled. Jäger & Kunz (2005) confirmed Roth's suspicions and matched the lectotype to specimens from Tanzania. Thus, the species is not native and most likely does not occur in the Nearctic region.

Keyserling (1884) described *O. giganteus*, *O. concolor* and *O. abnormis* from New Mexico, USA. The name *abnormis* was preoccupied by *Sparassus abnormis* Blackwall 1866 and the species was given the new name *Olios foxi* by Roewer (1951). *Olios concolor* and *O. giganteus* were synonymized with *O. fasciculatus* by Banks (1893) and the latter removed from this synonymy by Roth (1988).

Olios peninsulanus was described by Banks (1898), based on a male and a female from San Jose del Cabo, Baja California, Mexico. Chamberlin (1919) described *O. schistus* from Claremont, Los Angeles, USA, and a few years later (1924), *O. naturalisticus*, *O. positivus*, *O. scepticus* and *O. pragmaticus* from the Gulf of California (Tiburon Island, San Francisco Island, Ceralba Island, and San Lorenzo Island, respectively), Mexico. *Olios pragmaticus* was synonymized with *O. fasciculatus* by Fox (1937) who revised the Nearctic fauna of Sparassidae and described three new species: *Olios albinus*, from Phoenix, Arizona, *O. bibranchiatus*, from Madera Canyon, Arizona, and *O. mohavensis*, from the Mojave desert, California. He also recorded the presence of two non native sparassid species: *Heteropoda venatoria* (Linnaeus 1767), a widely distributed pantropical species, and *Pseudosparianthis cubana* Banks 1909, originally described from Cuba, in Southwestern USA and Florida, respectively. *Olios mohavensis* was recently transferred to *Macrinus* by Rheims (2010).

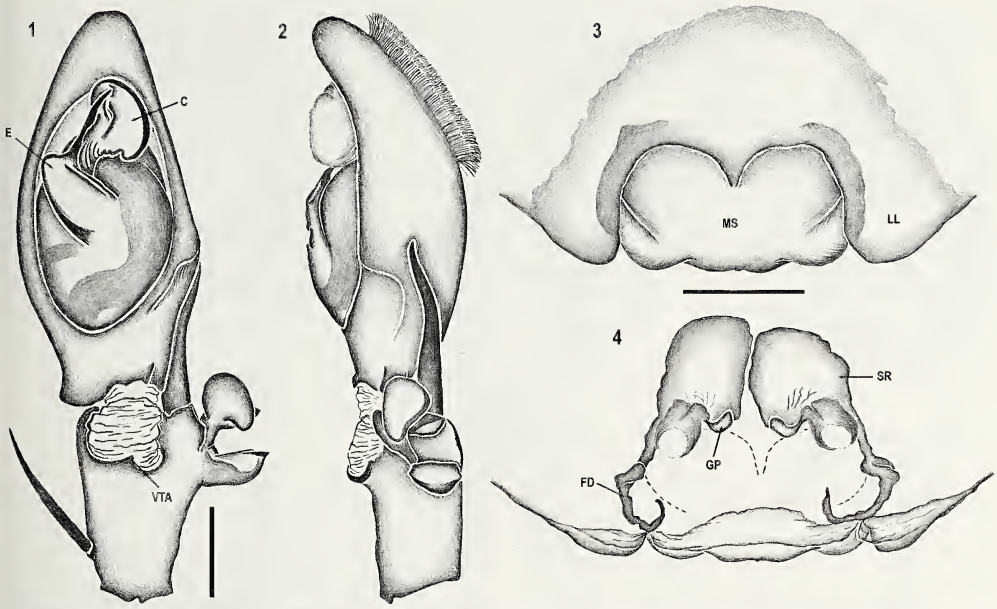
In this paper I present the taxonomic revision of the native Nearctic fauna of Sparassidae. All species, currently included in the genus *Olios*, are redescribed and illustrated. Comparisons between these species and the type species of *Olios*, *Olios argelasius* (Walckenaer 1805), show that none of them are congeneric and that true *Olios* does not occur in the Nearctic region. Nevertheless, the correct placement of these species in new genera will only be possible after a more thorough revision of the Nearctic and Neotropical fauna, especially that of Mexico and Central America.

METHODS

The examined material is deposited in the following institutions (abbreviation and curator in parentheses): American Museum of Natural History, New York (AMNH, N.I. Platnick); California Academy of Sciences, San Francisco (CAS, C.E. Griswold); Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ, G. Giribet); National Museum of Natural History, Smithsonian Institution, Washington DC (USNM, J.A. Coddington).

Morphological observations and illustrations were made using a Leica MZ12 stereomicroscope with a camera lucida. Measurements were taken with a micrometric ocular and are given in millimeters. Female genitalia were observed in clove oil after dissection.

The format of descriptions follows that used in Rheims (2007). Spine notation follows that of Petrunkevitch (1925).



Figures 1–4.—*Olios bibranchiatus*. 1. Male, left palp, ventral view; 2. Same, retrolateral view; 3. Female, epigynum, ventral view; 4. Same, vulva, dorsal view (C = conductor, E = embolus, FD = fertilization duct, GP = glandular projection, LL = lateral lobes, MS = median septum, SR = seminal receptacle, VTA = ventral tibial apophysis). Scale lines: 1mm.

Leg measurements are listed as: total length (femur, patella, tibia, metatarsus, tarsus); eye diameters as: AME, ALE, PME, PLE; interdistances as: AME–AME, AME–ALE, PME–PME, PME–PLE, AME–PME, ALE–PLE. Abbreviations used throughout the text: ALE, anterior lateral eyes; AME, anterior median eyes; d, dorsal; p, prolateral; PLE, posterior lateral eyes; PME, posterior median eyes; r, retrolateral; RTA, retrolateral tibial apophysis; v, ventral; VTA, ventral tibial apophysis; mi, miles.

TAXONOMY

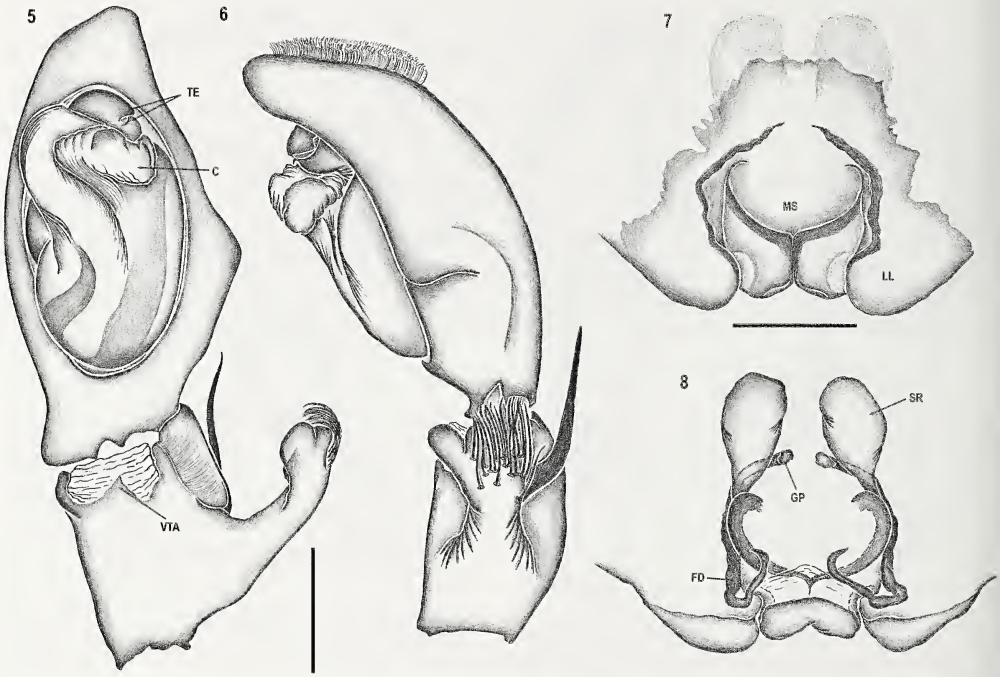
Olios bibranchiatus Fox 1937
Figs. 1–4, 17

Olios bibranchiatus Fox 1937:470, figs. 6, 8 (Male holotype from Madera Canyon, Santa Rita Mountains, Pima County, Arizona, USA, May 1898, E.A. Schwartz leg. and female allotype from Santa Fé , 35°41′N, 105°56′W, New Mexico, USA, deposited in USNM, examined; two male and three female paratypes from Oro Blanco Mountains, 12 mi from Nogales, 31°36′N, 110°59′W, Arizona, USA, July1937, deposited in AMNH, examined). Platnick 2010.

Additional material examined.—USA: *New Mexico*: 1 female, Santa Fé (35°41′N, 105°56′W) (USNM). *Arizona*: 1 male, Sedona (34°52′N, 111°45′W) (AMNH); 2 males, Yarnell (34°13′N, 112°44′W) (AMNH); 1 male, Santa Catalina Mountains, Peppersauce Cave Canyon (32°26′N, 110°47′W) (AMNH); 1 male, Pima County, Tucson (32°13′N, 110°55′W) (CAS); 1 male, Cochise County, Paradise Chiricahua Mountains (31°55′N, 109°22′W) (CAS); 1 male, Portal (31°54′N, 109°08′W) (AMNH); 1 male, Santa Rita Mountains (31°43′N, 110°52′W) (USNM); 1 male, same locality (AMNH); 1 male, Douglas (31°20′N, 109°32′W) (AMNH). MEXICO: *Sonora*: 1 female, 6 mi W Bahía San Carlos, "Los Algodones" (CAS); 1 male, 10 mi W Alamos (AMNH); 1 male, Hermosillo (29°04′N, 110°58′W) (AMNH); 1 male, Guaymas (27°59′N, 110°54′W) (AMNH). *Durango*: 1 male, vicinity of Durango (24°01′N, 104°40′W) (CAS). *Nayarit*: male, 1 female and 1 juvenile, Jesus Maria (22°15′N, 104°31′W) (AMNH); 2 males, San Blas, Mantauchen Beach (21°32′N, 105°17′W) (AMNH); 1 male and 2 females, 7 mi E San Blas (CAS); 1 female, Tepic (21°30′N, 104°53′W) (AMNH). *Jalisco*: 1 male and 3 females, Jalisco (21°26′N, 104°54′W) (AMNH); 1 male, Compostela (21°14′N, 104°53′W) (AMNH); 1 male, Yalapa (20°28′N, 105°25′W) (AMNH).

Distribution.—USA to western Mexico.

Diagnosis.—*Olios bibranchiatus* Fox 1937 is distinguished from the remaining Nearctic species by the RTA, with a horizontally bifid ventral branch (Figs. 1, 2) and by the embolus with a wide base and slender tip in the male palp (Fig. 1); by the subrectangular median septum in the female epigynum being wider than long (Fig. 3); and by the short glandular projection in the female vulva (Fig. 4).



Figures 5–8.—*Olios peninsulanus*. 5. Male, left palp, ventral view; 6. Same, retrolateral view; 7. Female, epigynum, ventral view; 8. Same, vulva, dorsal view (C = conductor; FD = fertilization duct; GP = glandular projection; LL = lateral lobes; MS = median septum; SR = seminal receptacle; TE = tip of embolus; VTA = ventral tibial apophysis). Scale lines: 1mm.

Redescription.—*Holotype male, USNM:* Prosoma, legs and pedipalps brownish orange. Sternum brownish orange with brown margins. Labium brown, distally yellow. Endites brownish orange, distally lighter. Opisthosoma brownish gray. Total length 21.2. Prosoma: 10.2 long, 8.0 wide. Opisthosoma: 10.0 long, 6.8 wide. Chelicerae with two promarginal and four retromarginal teeth, the basal one smaller. Internal margin at fang base with 6 strong setae. Eye diameters: 0.52, 0.48, 0.36, 0.44; interdistances: 0.38, 0.16, 0.60, 0.70, 0.36, 0.38. Leg measurements (2143): I: 40.0 (10.8, 4.0, 10.6, 11.0, 3.6); II: 49.6 (13.6, 5.2, 13.0, 14.0, 3.8); III: 33.4 (10.0, 3.8, 8.2, 8.6, 2.8); IV: 40.0 (12.0, 3.8, 10.2, 11.0, 3.0). Trochanter notched. Metatarsi I–IV with dorsal trilobate membrane with median hook as large as lateral projections. Spination: femora I–III: p1-1-1; d0-1-1; r1-1-1; femur IV: p1-1-1; d 0-1-1; r0-0-1; tibiae I–IV: p1-0-1; d0-0-1; r1-0-1; v2-2-0; metatarsi I–III: p1-1-0; r1-1-0; v2-2-0; metatarsus IV: p1-1-1; r1-1-1; v2-2-0. Palp: tibia half cymbium length with small VTA and one prolateral spine; RTA distal with long, spine-like dorsal branch and horizontally bifid branch; cymbium slightly elongate with dorsal scopula and large rounded alveolus; tegulum ring-like with massive conductor, originating from the center; embolus very wide at base and distally slender (Figs. 1, 2).

Allotype female, USNM: Coloration pattern as in male. Total length 22.4. Prosoma: 10.2 long, 9.0 wide. Opisthosoma: 13.4 long, 9.6 wide. Chelicerae as in male. Eye diameters: 0.60, 0.50, 0.38, 0.44; interdistances: 0.50, 0.26, 0.92, 0.90, 0.56, 0.60. Leg measurements (2143): I: 38.4 (11.0, 5.0, 10.0, 9.4, 3.0); II: 42.0 (12.4, 5.4, 10.4, 10.8, 3.0); III: 30.6 (8.8, 4.4, 7.2, 7.8, 2.4); IV: 35.0 (10.2, 4.4, 8.6, 9.2, 2.6). Trochanter as in male. Trilobate membrane as in male. Spination as in male except tibiae I–IV: d0. Epigynum: lateral borders simple, with no projections; medium septum wider than long with pair of antero-lateral copulatory openings (Fig. 3). Vulva: copulation duct short, opening to large globular, membranous seminal receptacle (= spermatheca); glandular projection short and small; fertilization ducts very long and slender (Fig. 4).

Variation.—Males (n = 5): total length 9.5–13.6; prosoma 4.6–6.1; femur I 6.6–9.5. Females (n = 4): total length 12.3–18.0; prosoma 4.3–6.0; femur I 5.7–8.0.

Olios peninsulanus Banks 1898
Figs. 5–8, 18

Olios peninsulanus Banks 1898:266, plate 16, fig. 19 (One male and two female syntypes from San Jose del Cabo, 23°03'N, 109°41'W, Baja California, Mexico, N. Banks leg., deposited in MCZ 22591, examined). Platnick 2010.

Olios schistus Chamberlin 1919:10, plate 4, figs. 2, 3 (Male holotype from Claremont, 34°05′N, 117°43′W, Los Angeles County, California, USA, April 1913, R.V. Chamberlin leg., deposited in MCZ 354, examined; one female paratype from the same locality as holotype, W.A. Hilton leg., deposited in MCZ 355, examined). Fox 1937:469, figs. 7, 10; Platnick 2010. **New synonymy**

Olios scepticus Chamberlin 1924:658, fig. 120 (Female holotype from Ceralba Island, 24°23′N, 109°45′W, Gulf of California, Mexico, 6 June 1921, J.C. Chamberlin leg., deposited in CAS 1440, examined; female paratype from Ceralba Island, 24°23′N, 109°45′W, Gulf of California, Mexico, 6 June 1921, J.C. Chamberlin leg., deposited in MCZ 1209, examined). Platnick 2010. **New synonymy**

Olios positivus Chamberlin 1924:657, fig. 99 (Female holotype from San Francisco Island, Gulf of California, Mexico, 30 May 1921, J.C. Chamberlin leg., deposited in CAS 1439, examined; immature female paratype from San Francisco Island, Gulf of California, Mexico, 30 May 1921, J.C. Chamberlin leg., deposited in MCZ 22727, examined). Platnick 2010. **New synonymy**

Additional material examined.—USA: *California*: 1 female, Los Angeles County, Arcadia, 34°08′N, 118°02′W (AMNH); 3 males and 2 females, Claremont (34°05′N, 117°43′W) (AMNH); 1 male, same locality (USNM); 1 female, Los Angeles (34°03′N, 118°14′W) (USNM); 1 male, same locality (AMNH); 1 male and 1 juvenile, 3 miles W Santa Monica (AMNH); 2 males and 1 juvenile, Toponga Can (34°N; 118°W) (AMNH); 1 female, La Habra (33°55′N, 117°56′W) (CAS); 1 female, San Jacinto (33°47′N, 116°57′W) (USNM); 1 male, Catalina Island (33°22′N, 118°26′W) (CAS); 2 males, La Cresta (32°48′N, 116°51′W) (AMNH); 5 males and 1 female, San Diego (32°42′N, 117°09′W) (USNM); 1 male, same locality (AMNH); 2 males, San Diego, Lakeside (USNM). MEXICO: *Baja California*: 1 male (USNM); 1 female, El Tarte (USNM); 1 female and 1 juvenile, same locality (CAS); 2 males, Río San Salvador, at Highway 3, Malise flowing Creek (31°52′24″N, 116°05′27″W) (CAS); 1 male, St. Martin Island (30°29′N, 116°06′W) (CAS); 1 male and 1 female, El Rosario (30°03′N, 115°43′W) (AMNH); 1 male, Penjamo (29°58′N, 115°07′W) (CAS); 1 male, Santa Inez (29°41′N, 114°42′W) (CAS); 1 male, San Jose, Meling Ranch (29°32′N, 114°42′W) (AMNH); 1 female, Playa Lobos (CAS); 2 males, Isla Angel de la Guarda, Puerto Refúgio, on north end (29°16′N, 113°24′W) (CAS); 1 female, 19 mi W Santa Teresa (28°04′N, 113°07′W) (CAS). *Baja California Sur*: 2 females, 1.7 km W Guerrero Negro, on road to Estero de San Jose (CAS); 1 male and 1 juvenile, Todos Santos (29°30′N, 114°45′W) (AMNH); 3 males, 28 mi SSE Todos Santos (CAS); 1 female, Punta Palmilla (CAS); 1 female, 38 km N Guerrero Negro, turnoff at km 90 on Mexico Highway 1 (CAS); 1 male, 6 km SE San Antonio (CAS); 1 male, Loreto (26°01′N, 111°20′W) (AMNH); 1 female, El Mesguital (25°45′N, 100°15′W) (CAS); 1 female, 12 km W Santiago, Rancho Mata Gorda (CAS); 1 male, La Paz (24°10′N, 110°17′W) (CAS); 1 female, same locality (AMNH); 1 female and 2 juveniles, E La Paz (CAS); 1 male, E Sombrero Trailer Park (CAS); 1 female and 1 juvenile, E Valle Perdido (CAS); 1 female, 0.5 mi N Miraflores (CAS); 1 female, 7 mi N Santa Anita, on Highway Sur (CAS); 1 male and 2 females, San Jose del Cabo (23°03′N, 109°40′W) (USNM); 1 female, Cabo San Lucas (22°52′N, 109°54′W) (CAS). *Nayarit*: 1 female, 7.3 mi E San Blas (CAS).

Distribution.—Southwestern USA and Baja California in Mexico.

Diagnosis.—*Olios peninsulanus* Banks 1898 is distinguished from the remaining Nearctic species by the RTA with a long ventral branch with strong hairs subdistally (Figs. 5, 6) in the male palp, by the median septum as long as wide with a pair of posterior lobes in the female epigynum (Fig. 7) and by the very long glandular projections in the female vulva (Fig. 8).

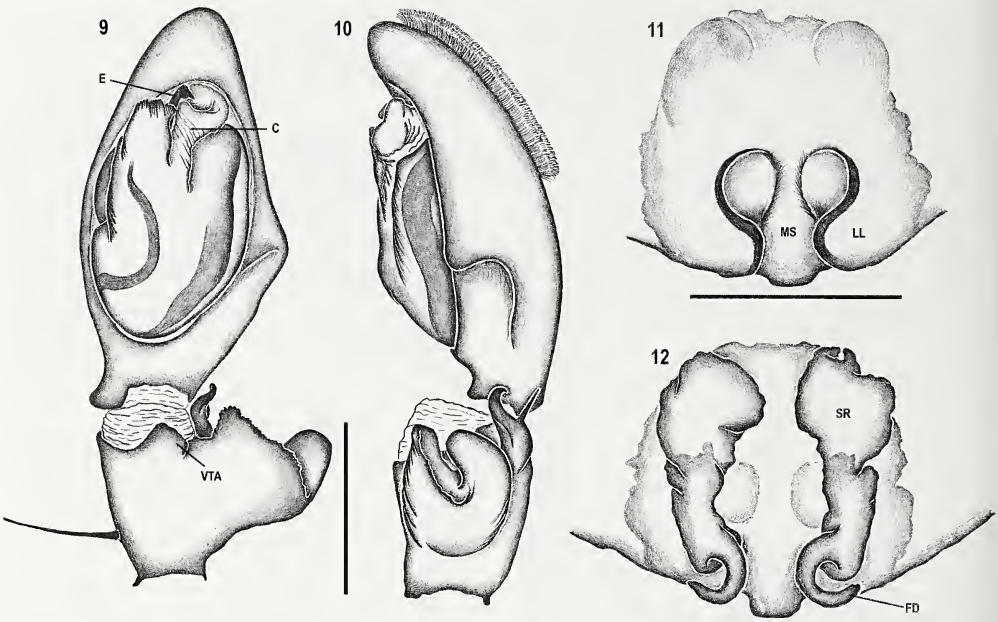
Redescription.—*Male (USNM):* Prosoma orange with small black spots at the base of setae on cephalic region. Chelicerae, legs and pedipalps pale orange. Sternum orange with darker margins. Labium and endites orange, distally pale orange. Opisthosoma brownish yellow. Dorsally mottled with small brown spots and with 3–4 medial chevrons on posterior half. Total length 13.0. Prosoma: 5.4 long, 6.0 wide. Opisthosoma: 7.6 long, 5.6 wide. Chelicerae with two promarginal and three retromarginal teeth, the most basal one smallest. Inner margin at base of fang with four strong setae. Eye diameters: 0.42, 0.38, 0.26, 0.34; interdistances: 0.36, 0.14, 0.56, 0.56, 0.34, 0.30. Leg measurements (2143): I: 30.2 (8.4, 3.4, 8.0, 8.0, 2.4); II: 34.0 (9.6, 3.6, 9.2, 8.8, 2.8); III: 23.8 (7.4, 3.0, 5.8, 5.6, 2.0); IV: 27.2 (7.6, 3.0, 7.0, 7.6, 2.0). Trochanter notched. Metatarsi I–IV with dorsal trilobate membrane with median hook as large as lateral projections. Spination: femora I–III: p1-1-1; d0-1-1; r1-1-1; femur IV: p1-1-1; d0-1-1; r0-1-1; tibia I: p1-0-1; r1-0-1; v2-2-0; tibiae II–IV: p1-0-1; d0-0-1; r1-0-1; v2-2-0; metatarsi I–III: p1-1-0; r1-1-0; v2-2-0; metatarsus IV: p1-1-1; r1-1-1; v2-2-0. Palp: tibia short, shorter than half cymbium length with small VTA and no spines (Fig. 5); RTA with long, spine-like dorsal branch and long ventral branch with many strong hairs subdistally (Figs. 5, 6); cymbium slightly elongate with dorsal scopula, slightly pronounced retrolateral bulge and large rounded alveolus; tegulum ring-like with massive conductor originating at center; embolus wide with bifid tip (Fig. 5).

Female (USNM): Coloration pattern as in male, slightly darker. Total length 20.0. Prosoma: 7.6 long, 7.6 wide. Opisthosoma: 11.2 long, 9.0 wide. Chelicerae with two promarginal and four retromarginal teeth, the basal one smallest. Eye diameters: 0.50, 0.44, 0.34, 0.34; interdistances: 0.50, 0.24, 0.80, 0.82, 0.48, 0.44. Leg measurements (2143): I: 29.4 (8.2, 4.2, 6.8, 7.6, 2.6); II: 32.2 (9.2, 4.2, 8.0, 8.0, 2.8); III: 23.2 (7.2, 3.4, 5.2, 5.4, 2.0); IV: 26.0 (8.0, 3.4, 6.0, 6.4, 2.2). Trochanter as in male. Trilobate membrane as in male. Spination as in male, except tibiae II–IV: d0. Epigynum: lateral lobes simple, without projections; median septum as long as wide with two posterior lobes (Fig. 7). Vulva: membranous seminal receptacle oval; glandular projections slender, almost as long as seminal receptacle; fertilization ducts long (Fig. 8).

Variation.—Males (n = 10): total length 6.2–8.7; prosoma 2.5–4.2; femur I 3.7–5.7. Females (n = 10): total length 7.8–11.3; prosoma 2.9–4.6; femur I 3.1–5.4.

Olios naturalisticus Chamberlin 1924
Figs. 9–12, 19

Olios abnormis Keyserling 1884:679, plate 21, fig. 27 (Male holotype from PW, New Mexico, USA, deposited in



Figures 9–12.—*Olios naturalisticus* Chamberlin. 9. Male, left palp, ventral view; 10. Same, retrolateral view; 11. Female, epigynum, ventral view; 12. Same, vulva, dorsal view (C = conductor; E = embolus; FD = fertilization duct; LL = lateral lobes; MS = median septum; SR = seminal receptacle; VTA = ventral tibial apophysis). Scale lines: 1mm.

USNM, examined). Preoccupied by Blackwall 1866, sub *Sparassus*.

Olios naturalisticus Chamberlin 1924:659, fig. 101 (Female holotype from southeastern corner of Tiburon Island, 29°00′N, 112°25′W, Baja California, Mexico, 4 July 1921, J.C. Chamberlin leg., deposited in CAS 1441, examined; one immature female paratype from Patos Island, 29°16′N, 112°27′W, Baja California, Mexico, 23 April 1921, J.C. Chamberlin leg., deposited in MCZ 1210, examined). Platnick 2010.

Olios albinus Fox 1937:473, fig. 3 (Female holotype from Phoenix, 33°26′N, 112°04′W, Arizona, USA, May 1935, R.V. Chamberlin, deposited in USNM). Platnick 2010. **New synonymy**

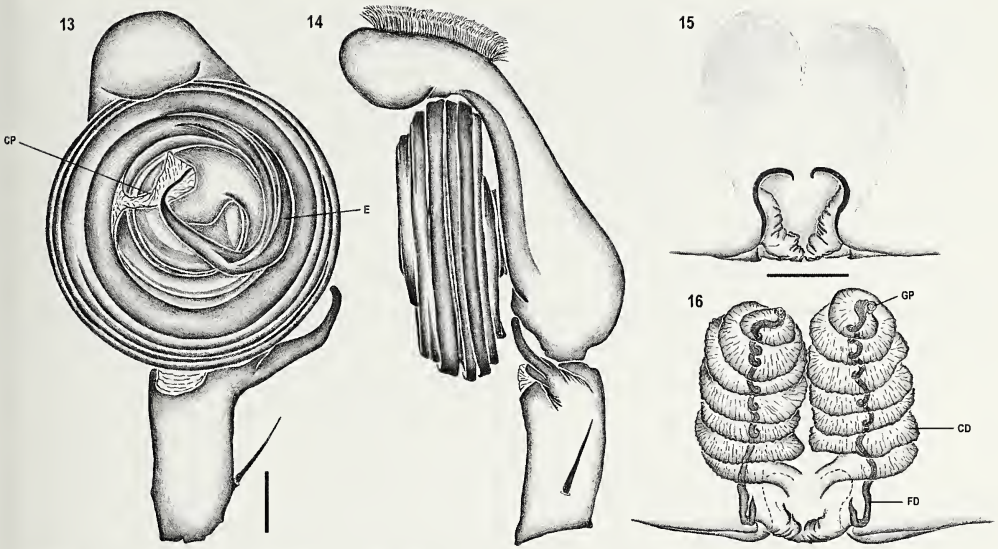
Olios foxi Roewer 1951 (replacement name for *O. abnormis* Keyserling 1884, preoccupied by Blackwall 1866, sub *Sparassus*). Platnick 2010. **New synonymy**

Additional material examined.—USA: *Arizona*: 1 male, Mohave County, 15 mi W Davis Camp (CAS); 1 female, Phoenix (33°26′N, 112°04′W) (AMNH); 1 female, Yuma County, Mittry Lake (32°49′N, 114°29′W) (AMNH); 1 female, Yuma County, Morellos Dam (32°43′N, 114°37′W) (AMNH); 1 male and 1 female, Yuma (32°43′N, 114°37′W) (CAS); 2 males and 4 females, same locality (AMNH); 1 male, Babaquivary Mountains, Kito Peak Ringon (32°24′N, 111°57′W) (AMNH); 1 male, Babaquivary Mountains, Forestry Cabin (AMNH); 1 female, Organ Pipe (32°16′N, 112°44′W) (CAS); 2 males, Pima County, Tucson (32°13′N, 110°55′W) (AMNH); 19 males, Cochise County, Portal (31°54′N, 109°08′W) (AMNH). *California*: 1 male, Los Angeles County, Los Angeles (34°03′N, 118°14′W) (USNM); 2 females, Riverside County, Indian Wells (33°43′N, 116°18′W) (AMNH); 1 male, Blythe (33°36′N, 114°35′W) (CAS). MEXICO: *Baja California*: 1 female, San Felipe (31°01′N, 114°50′W) (AMNH). *Sonora*, 1 female, 1 mi W Bahía San Carlos (CAS); 1 male, same locality (AMNH); 1 female, Desemboque (29°30′N, 112°22′W) (AMNH); 2 males, four females and 2 juveniles, Guaymas (27°59′N, 110°54′W) (AMNH); 1 female, 17 mi S Navojoa (CAS); 1 male, 15–20 km E Baviacora (AMNH).

Distribution.—Southwestern USA to Northwestern Mexico.

Diagnosis.—*Olios naturalisticus* Chamberlin is distinguished from the remaining Nearctic species by the RTA with massive, transversally bifid ventral branch and short, distally bifid dorsal branch (Figs. 9, 10) in the male palp; by the female epigynum with median septum with pair of large anterior atria (Fig. 11); and by the female vulva with thick and shorter fertilization ducts (Fig. 12).

Redescription.—*Male (USNM):* Prosoma pale orange with black stripes extending backwards from PLE and black U-shaped stripe at base of cephalic region. Chelicerae pale orange with few black spots at the base of setae. Pedipalps



Figures 13–16.—*Olios giganteus* Keyserling. 13. Male, left palp, ventral view; 14. Same, retrolateral view; 15. Female, epigynum, ventral view; 16. Same, vulva, dorsal view (CD = copulatory duct; CP = conductor-like projection; E = embolus; FD = fertilization duct; GP = glandular projection). Scale lines: 1mm.

pale orange. Legs pale orange mottled with few brown spots. Sternum yellow with pale orange margins, mottled with few black spots. Labium and endites pale orange, distally cream colored. Opisthosoma brownish gray. Dorsally with median chevrons and mottled with brown spots anteriorly. Ventrally mottled with brown spots. Total length 14.0. Prosoma: 6.0 long, 6.4 wide. Opisthosoma: 7.6 long, 5.4 wide. Chelicerae with two promarginal and four retromarginal teeth, the most basal smaller. Inner margin at base of fang with four strong setae. Eye diameters: 0.46, 0.34, 0.30, 0.36; interdistances: 0.36, 0.18, 0.64, 0.62, 0.50, 0.40. Leg measurements (2143): I: 31.0 (8.8, 3.2, 8.2, 8.2, 2.6); II: 33.6 (9.6, 3.8, 9.2, 8.6, 2.4); III: 24.00 (7.4, 3.0, 5.8, 5.8, 2.0); IV: 28.2 (8.4, 3.0, 7.2, 7.4, 2.2). Trochanter notched. Metatarsi I–IV with dorsal trilobate membrane with median hook as large as lateral projections. Spination: femora I–III: p1-1-1; d0-1-1; r1-1-1; femur IV: p1-1-1; d0-1-1; r0-1-1; tibiae I–IV: p1-0-1; d0-0-1; r1-0-1; v2-2-0; metatarsi I–III: p1-1-0; r1-1-0; v2-2-0; metatarsus IV: p1-1-1; r1-1-1; v2-2-0. Palp: tibia short, shorter than half cymbium length, with small VTA and one prolateral spine (Fig. 9); RTA distal, with short and bifid dorsal branch and massive, transversally bifid ventral branch (Fig. 10); cymbium slightly elongate with dorsal scopulae and large, rounded alveolus; tegulum ring-like with massive conductor, originating at center; embolus with slightly elongate, widened base and short, spine-like tip (Fig. 9).

Female (AMNH): Coloration pattern as in male. Total length 10.0. Prosoma: 3.3 long, 3.9 wide. Opisthosoma: 6.8 long, 5.5 wide. Chelicerae as in male. Eye diameters: 0.30, 0.22, 0.18, 0.22; interdistances: 0.20, 0.10, 0.42, 0.38, 0.22, 0.16. Trochanter notched. Metatarsi I–IV with dorsal trilobate membrane with median hook as large as lateral projections. Leg measurements (2143): I: 14.4 (4.0, 1.9, 3.6, 3.7, 1.2); II: 15.6 (4.6, 2.0, 3.9, 3.9, 1.2); III: 11.1 (3.4, 1.5, 2.7, 2.5, 1.0); IV: 13.5 (4.0, 1.7, 3.2, 3.5, 1.1). Spination as in male except tibiae I–IV: d0. Epigynum: lateral borders simple, without projections; median septum anteriorly narrow with two large lateral atria, bearing copulatory openings (Fig. 11). Vulva: copulation ducts inconspicuous; membranous seminal receptacle large and irregular; glandular projection very small and ventral, not seen in dorsal view; fertilization ducts short and thick (Fig. 12).

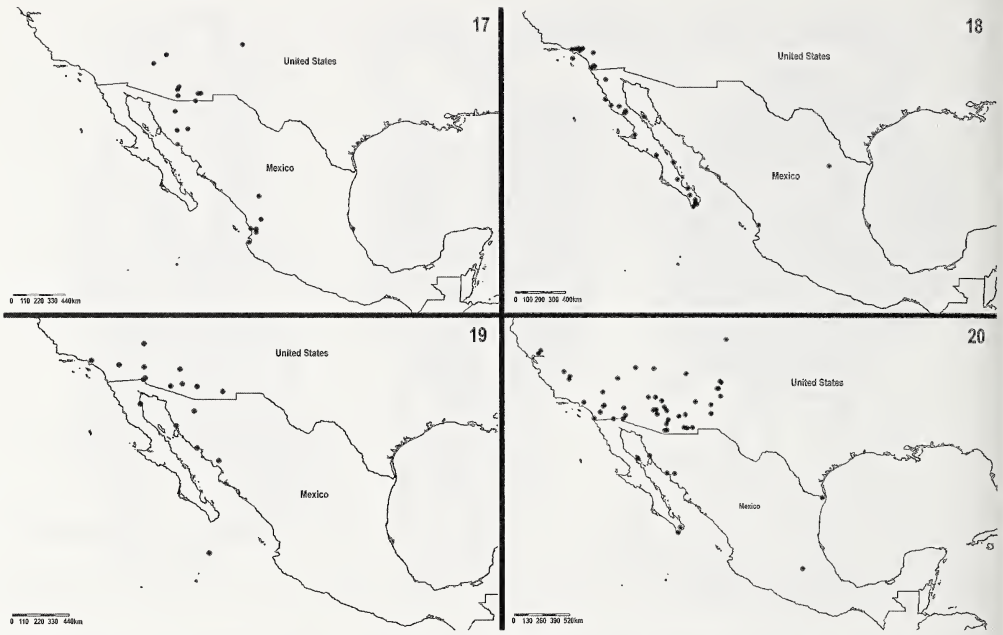
Variation.—Males (n = 8): total length 7.4–9.0; prosoma 3.5–4.0; femur I 4.8–5.4. Females (n = 5): total length 8.2–9.1; prosoma 3.4–4.2; femur I 4.0–5.2.

Olios giganteus Keyserling 1884
Figs. 13–16, 20

Olios giganteus Keyserling 1884:681, plate 21, fig. 28 (Female holotype from Punta del Agua, 34°36′N, 106°16′W, New Mexico, USA, deposited in USNM, examined). Roth 1988:36 (removed from syn. of *O. fasciculatus*). Platnick 2010.

Olios concolor Keyserling 1884:682, plate 21, fig. 29 (Male holotype from Punta del Agua, 34°36′N, 106°16′W, New Mexico, USA, deposited in USNM, examined). Platnick 2010. **New synonymy**

Olios pragmaticus Chamberlin 1924:659, fig. 102 (Female holotype from South San Lorenzo Island, Baja California, Mexico, 9 May 1921, J.C. Chamberlin leg., deposited in CAS 1442, examined). Platnick 2010. **New synonymy**



Figures 17–20.—Distribution maps. 17. *Olios bibranchiatus*; 18. *Olios peninsulanus*; 19. *Olios naturalisticus*; 20. *Olios giganteus*.

Additional material examined.—USA: *Arizona*: 1 female, Los Cabezas (AMNH); 1 female and 1 juvenile, Colorado, Septinel Rock (39°32′N, 105°46′W) (AMNH); 1 male and 3 juveniles, Mariposa County, Cove Creek (36°33′N, 109°13′W) (CAS); 1 male, Comp Verde (34°33′N, 111°51′W) (AMNH); 1 female, Prescot (34°32′N, 112°28′W) (AMNH); 1 male, Gila County, 2 mi NE Payson (AMNH); 1 female, near Roosevelt Dam (33°41′N, 111°06′W) (AMNH); 1 male, Phoenix (33°26′N, 112°04′W) (AMNH); 1 female, 30 mi N Mesa on Verde (AMNH); 1 female, Mariposa County, Mesa (33°25′N, 111°49′W) (USNM); 2 males, 2 females and 1 juvenile, same locality (CAS); 1 female, Gila County, 13 miles W Miami (AMNH); 1 female, Sacaton (33°04′N, 111°44′W) (USNM); 1 male, Greenlee County, Clifton (33°03′N, 109°17′W) (AMNH); 1 female, Yuma County, Martinez Lake (32°58′N, 114°28′W) (AMNH); 1 female, Pima County, Base of Tortula Mountains (32°53′N, 109°49′W) (CAS); 2 females, Fort Yuma (32°44′N, 114°37′W) (USNM); 1 male and 1 female, Yuma County, Yuma (32°43′N, 114°37′W) (CAS); 2 males, same locality (AMNH); 1 female, Oracle (32°36′N, 110°46′W) (USNM); 1 male, Pima County, Tucson (32°13′N, 110°55′W) (CAS); 1 female, same locality (USNM); 1 female, same locality (AMNH); 1 male, Pima County, Avra Valley, 50 km WNW Tucson (USNM); 1 male, Tucson, Madera Canyon (AMNH); 1 female, Tucson, Sabino Canyon (AMNH); 1 female, Cochise County, Massai Point, Chiracahua Mountains (31°55′N, 109°22′W) (AMNH); 12 males, 3 females and 1 juvenile, Cochise County, Portal (31°54′N, 109°08′W) (AMNH); 2 males and 2 females, Portal, SW Research Station (AMNH); 1 male, Santa Rita Mountains, Madera Canyon (31°43′N, 110°52′W) (USNM); 2 males and 1 female, Big Rock Camp, Madera Canyon (AMNH); 1 male and 2 females, Pima County, Sopori School (31°39′N, 111°03′W) (AMNH). *California*: 1 female, Yolo County, Davis (38°32′N, 121°44′W (CAS); 2 females, Solano County, Gates Canyon (38°18′N, 121°54′W) (CAS); 1 male and 1 female, Fresno County, Fresno (36°44′N, 119°46′W) (CAS) 1 female, same locality (AMNH); 10 males, 8 females and 5 juveniles, Tulare County, Ash Mountain, Kaweah Power Station, 40 mi NE Visalia (CAS); 1 female, Tulare County, Creighton Ranch Native Conservancy Preserve, near Tipton (36°03′N, 119°18′W) (CAS); 1 male, San Bernardino County, Mountain Home Creek (AMNH); 1 male, San Bernardino County, State Park, Mitchell Cavern (AMNH); 1 female, El Monte (34°04′N, 118°01′W) (USNM); 1 female, Riverside County, Pushwalla Palms (33°49′N, 116°16′W) (AMNH); 1 female, Riverside County, Palm Desert (33°43′N, 116°22′W) (AMNH); 1 female, Riverside County, Blythe (33°36′N, 114°35′W) (CAS); 1 female, Warner Springs (33°16′N, 116°38′W) (USNM); 1 female, San Diego (32°42′N, 117°09′W) (USNM); 1 female, Calexico, 1 mi W Calexico post office (32°40′N, 115°29′W) (CAS). *Utah*: 4 females, Saint George (37°06′N, 113°34′W) (AMNH); 4 males, 4 females and 5 juveniles, Zion National Park (37°N, 112°W) (AMNH). *Nevada*: 1 male, 1 female and 1 juvenile, Las Vegas (36°10′N, 115°08′W) (AMNH). *New Mexico*: 1 male, Los Alamos

County, Juniper (35°53′N, 106°18′W) (AMNH); 1 male, Los Alamos County, White Rock (35°49′N, 106°12′W) (AMNH); 2 females, Sandoval County, Placitas (35°18′N, 106°25′W) (AMNH); 1 male and 1 female, Bernalillo County (AMNH); 1 female, Punta del Agua (34°36′N, 106°16′W) (USNM); 1 female, Catron County (34°09′N, 108°25′W) (AMNH); 1 female, Socorro, 3 mi E Cienega Ranch (33°52′N, 107°05′W) (AMNH); 1 female, Sierra County, Natural Forest, 9 km W Hillsboro Highway 90 (CAS); 1 male, Hidalgo, 30 km N Lordsburg (AMNH). *Texas*: 1 female, Brownsville (25°54′N, 97°29′W) (AMNH). MEXICO: *Baja California*: 1 female, Isla Angel de la Guarda, South End (29°16′N, 113°24′W) (CAS); 1 male, 6 mi N Santiago, on Highway Sur (CAS). *Baja California Sur*: 1 female, Miraflores (23°21′N, 109°45′W) (CAS); 1 male, Cabo San Lucas (22°52N, 109°54′W) (CAS); 1 female, 14 km E Mexico highway 9, on road to La Burrera (CAS); 1 female, Isla Espirito Santo, Playa La Bonanza (CAS). *Sonora*: 1 female, Desemboque (29°30′N, 112°22′W) (AMNH); 1 male, Guaymas, San Carlos Bay (27°59′N, 110°54′W) (AMNH); 1 female, Guyamas, Str. Albatross (USNM); 1 female, Agua Caliente (27°57′N, 110°13′W) (CAS).

Distribution.—Mainly Nearctic, occurring from southwestern United States to northern Mexico, with one single record from Sonora, central Mexico.

Diagnosis.—*Olios giganteus* Keyserling can be distinguished from the remaining Nearctic species by the elongate embolus, spiraled at least six times around small ring-like tegulum in the male palp (Figs. 13, 14) and by the female vulva with hyaline, spiraled copulation ducts and very long, slightly coiled fertilization ducts (Fig. 16).

Redescription.—*Male (USNM):* Prosoma orange brown, slightly darker at clypeus and with reddish brown fovea. Chelicerae dark reddish brown. Legs and pedipalps orange brown. Sternum orange with brown margins. Labium and endites brownish orange, distally cream colored. Opisthosoma brownish gray. Dorsally with conspicuous heart mark with brown margins and mottled with brown spots. Total length 25.0. Prosoma: 11.4 long, 10.8 wide. Opisthosoma: 12.4 long, 9.2 wide. Chelicerae with two promarginal and four retromarginal teeth, the most basal smaller. Inner margin, at base of fang, with 10 strong setae. Eye diameters: 0.74, 0.74, 0.56, 0.62; interdistances: 0.44, 0.16, 0.90, 0.94, 0.90, 0.64. Leg measurements (2143): I: 58.8 (16.4, 6.2, 15.6, 16.2, 4.4); II: 62.8 (17.8, 7.0, 16.8, 17.0, 4.2); III: 45.4 (14.4, 5.0, 12.6, 12.0, 3.4); IV: 52.8 (16.0, 5.4, 13.8, 14.2, 3.4). Trochanter notched. Metatarsi I–IV with dorsal trilobate membrane with median lobe as large as lateral projections. Spination: femora I–III: p1-1-1; d0-1-1; r1-1-1; femur IV: p1-1-1; d0-1-1; r0-0-1; tibiae I-IV: p1-0-1; d0-0-1; r1-0-1; v2-2-0; metatarsi I–IV: p1-1-0; r1-1-0; v2-2-0. Palp: tibia slightly longer than half cymbium length without VTA and one retrolateral spine (Figs. 13, 14); RTA simple, conical and elongate, slightly bent prolaterally (Fig. 13); cymbium with dorsal scopula (Fig. 14); tegulum small, ring-like; embolus very long and coiled with conductor-like projection arising subdistally (Figs. 13, 14).

Female (USNM): Coloration pattern as in male. Total length 31.6. Prosoma: 11.6 long, 11.2 wide. Opisthosoma: 20.0 long, 13.6 wide. Chelicerae as in male. Eye diameters: 0.46, 0.44, 0.32, 0.42; interdistances: 0.40, 0.24, 0.70, 0.84, 0.58, 0.46. Trochanter as in male. Trilobate membrane as in male. Leg measurements (2143): I: 44.4 (13.2, 5.8, 11.0, 11.2, 3.2); II: 47.0 (14.2, 6.0, 12.0, 11.6, 3.2); III: 35.8 (11.4, 5.2, 8.4, 8.4, 2.4); IV: 39.6 (12.2, 5.0, 9.6, 9.8, 3.0). Leg spination as in male. Epigynum: lateral borders simple, with no projections; median septum slightly longer than wide with crinkled latero-posterior margins (Fig. 15). Vulva: copulation ducts very long, hyaline and coiled around fertilization ducts; glandular projection small and rounded; fertilization ducts very long and slender, slightly coiled (Fig. 16).

Variation.—Males (n = 3): total length 11.3–29.4; prosoma 6.0–12.2; femur I 8.8–17.2. Females (n = 9): total length 14.6–48.0; prosoma 5.8–16.0; femur I 7.4–18.6.

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Testing species boundaries in *Pardosa sierra* (Araneae: Lycosidae) using female morphology and COI mtDNA

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Abstract. The wolf spider *Pardosa sierra* was described and illustrated by Banks in 1898 based on specimens from the Sierra de la Laguna, Baja California Sur. Later, two morphologically similar species, *P. atromedia* Banks 1904 from Claremont, California, and *P. sura* Chamberlin & Ivie 1941, also from California, were described. However, the latter two species were subsequently synonymized with *P. sierra*, due to similarities in male genitalia. In this study we test the species limits within this group. We suggest that the details of the epigynum are different enough among the genitalic morphs studied to consider them different species as originally designated. We conducted a morphological and genetic-distance analysis of a fragment of the cytochrome *c* oxidase subunit I gene sequences of some species of *lapidicina* group, as well as some sequences of *Pardosa astrigera* L. Koch 1878 from the GenBank database. Genetic analysis revealed greater genetic distances (GD) among haplotypes of *P. sierra*, *P. atromedia*, and *P. sura* (GD = 0.053–0.069) than with other species of the *lapidicina* group. Moreover, *P. sierra* was closest to *P. sura* (GD = 0.053), *P. sura* was closest to *P. vadosa* Barnes 1959 (GD = 0.040), and *P. atromedia* was closest to *P. steva* Barnes 1959 (GD = 0.052). Overall, morphological and genetic differences, and disjoint distributions, suggest that the synonymy of *P. sierra*, *P. atromedia*, and *P. sura* was in error, and that these "morphs" do indeed represent different species.

Keywords: Epigynal morphs, genetic distances, *lapidicina* group, taxonomy

Araneomorph spider taxonomy is based mainly on phenotypic variation of adult copulatory organs (Huber 2004; Astrin et al. 2006). These structures, the epigyna in females and pedipalps in males, usually have little intraspecific variation and conspicuous interspecific variation (Huber 2004). However, identification of spiders through morphology is not always straightforward. In some taxa, detailed morphological analyses of genitalia have failed to reveal diagnostic traits for one or both genders, and immatures further lack adult genitalia structures and are difficult to identify.

Additionally, some species show striking sexual dimorphism, exhibiting more than one genitalic morph as a result of environmental changes and/or reproductive isolation (Chang et al. 2007). In other cases, these genitalic morphs are so different that it is difficult to determine whether or not they belong to the same species (Huber 2004; Ubick et al. 2004).

These problems are particularly prevalent in the family Lycosidae and have been observed in different genera including *Trochosa*, *Pirata*, and *Pardosa* (Dondale & Redner 1981; Stratton & Uetz 1981; Stratton 1991; Reiskind & Cushing 1996; Milasowszky et al. 1998; Töpfer-Hofmann et al. 2000; Hepner & Milasowszky 2006; Dreyer & Brady 2008) and other genera (Scheffer et al. 1996; Parri et al. 1997; Miller et al. 1998). In the genus *Pardosa* this topic, mainly with regard to European groups, has received special attention from several authors (Tongiorgi 1966a; Tongiorgi 1966b; Holm &Kronestedt 1970; Hollander & Dijkstra 1974; Kronestedt 1981; Wunderlich 1984; Barthel & Helversen 1990; Kronestedt 1990, 1992, 2007; Chang et al. 2007). The American groups also contain species with closely similar genitalia (Barnes 1959; Lowrie & Dondale 1981; Dondale & Redner 1984). Thus, traditional taxonomy of the genus *Pardosa* has limitations for classifying many of its species.

Determining species limits can be facilitated through the use of molecular markers. In particular, genetic information derived from mitochondrial DNA is increasingly being used to supplement morphological data in taxonomy (Brower 1994; Hebert et al. 2003; Segraves & Pellmyr 2001; González et al. 2003; Froufe et al. 2003).

The wolf spider *Pardosa sierra* Banks 1898 (Araneae, Lycosidae) belongs to the *lapidicina* group of *Pardosa*. It is considered a widespread species from the southwestern region of the United States to Oaxaca and Veracruz in Mexico (Barnes 1959; Vogel 2004). These diurnal, ground-dwelling spiders are 5–9 mm. long and live in wetland boundaries of rocky places (Lowrie 1973; Punzo & Farmer 2006). Originally, *P. sierra* was described based on specimens from the Sierra de la Laguna in the southern part of the Baja California Peninsula illustrating a single female morph (Banks 1898). Later, Barnes (1959) revised the *lapidicina* group of *Pardosa* and synonymized *P. atromedia* Banks 1904 from Claremont, California, and *P. sura* Chamberlin & Ivie 1941 from California (36°16′N, 121°56′W) with *P. sierra*. Barnes (1959) also described another female morph from Sierra City, California, noting that this morph and one described by Banks (1898) were, in males, slightly different, but not enough to justify recognition as different species. However, no proof was provided that these morphs were all the same species.

To address this problem, we examined the genitalia of adult spiders collected from the Baja California Peninsula and the northern part of Mexico, in addition to specimens from several museum collections. Also, the cytochrome *c* oxidase subunit I (COI) gene was sequenced to detect differences at the molecular level. In the present study, we attempt a morphological and genetic separation of the different species included in *P. sierra*.

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Table 1.—Individuals sequenced in this work and information on sequences of *Pardosa astrigera* used to compare values of intraspecific and interspecific distances.

Species	Sampling location	Accession numbers	Voucher numbers	Individuals used
Pardosa valens	Sinaloa, Mexico	FJ546474	CAECIBG 1614	1♀ 1♂
	Chihuahua, Mexico	FJ546475	CAECIBG 1615	2♀
Pardosa steva	Sonora, Mexico	FJ546470	CAECIBG 1610	2♀ 2♂
	Nuevo León	FJ546471	CAECIBG 1611	2♀ 2♂
Pardosa sura	Chihuahua, Mexico	FJ546468	CAECIBG 1608	2♀ 1♂
	Durango, Mexico		CAECIBG 1616	2♀ 1♂
	Nuevo León, México	FJ546469	CAECIBG 1609	2♀ 1♂
Pardosa vadosa	Sonora, Mexico	FJ546472	CAECIBG 1612,	2♀ 1♂
	Chihuahua, Mexico	FJ546473	CAECIBG 1613	2♀ 1♂
Pardosa sierra	Ensenada, B. C., Mexico		CAECIBG 1617	2♀ 1♂
	Cadejé, B. C. S., Mexico	FJ546465	CAECIBG 1605	2♀ 1♂
	Sierra la Laguna, B. C. S., Mexico	FJ546464	CAECIBG 1604	3♀ 3♂
Pardosa atromedia	Rio Osos, California, USA	FJ546466	CAECIBG 1606	2♀
	Rio Osos, California, USA	FJ546467	CAECIBG 1607	1♂
Pardosa astrigera	China	AY836055.1	-	-
	China	AY836072.1	-	-

METHODS

Spider specimens.—We examined adults of "*P. sierra*" wolf spiders in four collections as follows: American Museum of Natural History, 60 specimens: 15 of *P. sierra*, 30 of *P. atromedia* and 15 of *P. sura*; California Academy of Sciences, 20 specimens: 10 of *P. sierra*, 5 of *P. atromedia* and 5 of *P. sura*; Darrell Ubick's personal collection: seven specimens of *P. sierra*; Centro de Investigaciones Biológicas del Noroeste: 150 specimens of *P. sierra*. Moreover, specimens of *P. sierra*, *P. atromedia*, and *P. sura* were collected from Baja California Sur, California and Chihuahua for morphological and molecular analysis; specimens of *Pardosa vadosa* Barnes 1959, *Pardosa valens* Barnes 1959, and *Pardosa steva* Lowrie & Gertsch 1955 were collected from Sonora, Chihuahua, and Sinaloa for molecular analysis (Table 1).

Voucher specimens and morphology.—Spiders, or parts of spiders, used for DNA extraction were stored in the Arachnological Collection at Centro de Investigaciones Biológicas del Noroeste (Table 1). Somatic measurements were made following the protocols described by Brady (1979) and Dreyer & Brady (2008). The measurements are reported here as mean ± standard deviation and maximum and minimum values in tables indicating the variability among species. We dissected and cleaned the genitalia of each specimen under a dissection microscope (60×). Epigynal characteristics include the following: hood, anterior limit of the epigynum, middle field, tissue between the hood and the transverse piece, copulatory openings, orifices for the male copulatory organ, transverse piece, tissue below the copulatory openings, which includes the crescent-shaped troughs, spermathecae, organs that produce germinal cells, copulatory ducts, and tubes connecting spermathecae with the copulatory openings. The main characteristics used for morphological comparison of individuals were the shape of the transverse piece, the middle field and the spermathecae (Figs. 2–4). For the male pedipalpal structure, the characters included total length and distal part of the cymbium, bulb size, embolus, conductor, and median and terminal apophysis. The characteristics used for morphological comparison among individuals were embolus, conductor and median accessory process, median and terminal apophysis (Figs. 5, 6, 7).

Abbreviations.—Body: sternum width (WE), sternum length (LE), posterior median eye width (PMEW), posterior lateral eye width (PLEW), posterior ocular quadrangle (POQ). Male palpal structures: embolus (E), median apophysis (MA), terminal apophysis (TA). Tibia (TP), femur (FP), total length of cymbium (BT), bulb length (Bx), distal part of the cymbium (AB). Female epigynal structures: fertilization ducts (FD), middle field length (MF), transverse piece (TP), spermathecae (SP), epigynum length (EpL), epigynum wide (EpW). Political units: County (Co.). Institutions: American Museum of Natural History, New York (AMNH); Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ); Centro de Investigaciones Biológicas del Noroeste, La Paz (CARCIB); California Academy of Science, San Francisco (CAS).

Electron microscopy.—Genitalia of three males and three females of each species were dissected and processed for scanning electron microscopy (SEM). Genitalia were processed overnight to degrade soft tissue with 100 µl DNA extraction buffer, 20 µl SDS, and two µl proteinase K in 0.2 ml tubes at 56° C. Subsequently, we stopped the enzymatic process by dehydrating the epigyna in 200 µl absolute alcohol, and prepared them for critical point drying. We coated samples with vanadium, examined them under SEM (Hitachi S-3000N), and digitalized images with Quartz PCI 5.0 software.

DNA extraction.—All specimens were preserved in 96% ethanol immediately after collection. The total genomic DNA (at least $n = 3$ in each species) was extracted from legs and sometimes half of the prosoma tissue of individual spiders as described by Aljanabi & Martinez (1997). The next step was to break down the tissue by placing it in a 1.5-ml Eppendorf tube with 410 µl extraction buffer (100 mM NaCl, 10 mM EDTA, 10 mM Tris at pH 8.0) and 90 µl 10% SDS, and macerating it with a plastic pestle. We added proteinase K (Sigma, #P2308, St. Louis, MO) to a final concentration of 10 U/ml and then incubated the mixture overnight at 56° C. Next we centrifuged

the tubes at 14000 rpm in a microcentrifuge (model 5414, Eppendorf) for 5 min. The supernatant was collected; 180 µl 5 M NaCl was added. After mixing and centrifuging again, we recovered the supernatant in a clean tube and cleaned it twice with a chloroform-isoamyl alcohol (24:1) solution. Finally, we precipitated DNA in the supernatant with absolute ethanol and washed it with 80% ethanol.

Polymerase chain reaction.—A 710-bp fragment of the COI gene was amplified by PCR with the following primers: COIP-L (5′-TAG AAA TAG GGG TTG GTG-3′) and COIP-R (5′-AAT GAA AAT GAG CTA CAA CA-3). These primers were designed from COI sequence of *Pardosa milvina* (Hentz 1844) previously reported (Greenstone et al. 2005 – GenBank sequence DQ072280). We performed PCR amplification in a 15 µl reaction volume containing approximately 50 ng genomic DNA, 0.40 mM each primer, 2.5 mM $MgCl_2$, 0.2 mM of each of the dNTP, 1×PCR buffer (Invitrogen, #Y02028, Carlsbad, California), and 0.5 U Taq polymerase (Invitrogen, #18038-042). Next, we ran PCR with initial denaturing step at 94° C for 4 min, followed by 35 cycles at 94° C for 30 s, 30 s at 52° C, and 30 s at 72° C, and a final step at 72° C for 10 min, in a programmable thermal cycler (BioRad Laboratories, Hercules, California).

DNA sequencing.—PCR amplification products were submitted for single-strand sequencing, using the ABI dye termination method in an ABI 377 automatic sequencer (Macrogen, Seoul, Korea). We translated each sequence in the amino acids, and no stop internal codons were found. We submitted all sequences to GenBank (Table 1). For comparative purposes, COI sequences of the three species were compared at two levels (intraspecific and interspecific) with sequences of some other *lapidicina* group species. We also used COI sequences of *P. astrigera* L. Koch 1878, because it has the most diverse dataset of haplotypes reported for a single species in the genus *Pardosa* (Chang et al. 2007).

Sequence analysis.—We made DNA sequence alignments of COI gene fragments from various spiders in the Chromas Pro program and ClustalX Windows interface v. 1.8 (Thompson et al. 1997), using these default parameters: gap opening cost = 15; gap extension cost = 6.66; delay divergent sequences = 30%; and DNA transition = 0.50). Sequences were truncated to 630 bp to avoid any bias in sequence alignment. We visually checked alignments using the BioEdit program (Hall 2007); final alignments were exported to a Nexus file using ClustalX Windows interface v. 1.8 (Thompson et al. 1997).

Molecular taxonomy.—We estimated taxa separation by calculating the interval between the lowest interspecific and the highest intraspecific observations (Astrin et al. 2006). A negative value indicates the numerical extent of overlap of both categories (intraspecific vs. interspecific distances). In this way, the gap range has to be zero or a negative value to consider an overlap that could be the degree of overlap between categories (intraspecific vs. interspecific) and is expressed by the proportion of data outside the gap range.

We used PAUP* ver. 4.0b10 (Swofford 2000) to calculate *p*-distance matrices as well as for construction of a neighbor-joining (NJ, Saitou & Nei 1987) tree, chosen to build a species identification tree (distinct from a tree chosen when striving for phylogenetic accuracy). As an exclusively algorithmic, phenetic procedure, NJ is fast at processing datasets, but produces only a single uncontested tree, often applied in molecular taxonomy (Paquin & Hedin 2004; Barrett & Hebert 2005; López-Legentil & Turon 2005; Markmann & Tautz 2005; Vences et al. 2005; Ward et al. 2005; Hajibabaei et al. 2006; Astrin et al. 2006; Smith et al. 2006). We used the Shapiro-Wilk test implemented in STATISTICA vs. 6 to test for a normal distribution of *p*-distance values.

SYSTEMATICS

Family Lycosidae Sundevall 1833
Subfamily Pardosinae Simon 1898
Genus *Pardosa* C.L. Koch 1847

Type species.—*Lycosa alacris* C.L. Koch 1833, designated by Charitonov (1932).

The *lapidicina* group.—This group presents a great many taxonomic difficulties because of its extreme homogeneity. All members of the *lapidicina* group possess essentially the same markings, although each species exhibits a considerable range in coloration from very pale to very dark individuals (Barnes 1959). The carapace is highest between the second and third eye row and slopes slightly to the posterior declivity in the posterior one-fifth of the carapace. The anterior median eyes are separated by approximately four-fifths of a diameter; the anterior laterals are three-fourths to one-half of the diameter of the anterior median eyes in size and separated from the latter by one-fifth of their diameter. The eyes of the second row are two to two and one-half times the diameter of the anterior median eyes. The eyes of the third row are only very slightly smaller than the eyes of the second row and are separated from the latter by one to two times the diameter of the eyes of the second row. The second eye row is one and one-half times the length of the first; the third eye row, twice the length of the first. The ocular area is wider than long. Order of leg length: 4:1:2:3 (Barnes 1959).

The structure of the male pedipalpal organ is the most valuable character for separating the species of the *lapidicina* group (Barnes 1959), but not in the case of our three species where the female genitalia showed the main differences among species.

After morphological study of specimens from collections, we found three morphs designated as *P. sierra* described by Banks 1898:374, pl. XVI, fig. 20 as *P. sierra*, *P. atromedia* described by Banks 1904:355, pl. XXXIX, fig. 32, and *P. sura* (with epigynum illustrated by Chamberlin & Ivie 1941:10, pl. V, fig. 61) and Barnes 1959, fig. 36 as a morph of *P. sierra*. *Pardosa sierra* was described from a collection from the Sierra de la Laguna (Banks 1898), but also was collected from other localities on the Baja California Peninsula. *Pardosa atromedia* was collected from California. *Pardosa sura* was collected in Mexico (Distrito Federal, Estado de Mexico, Chihuahua, and Puebla) and in the southwestern USA (Utah, Colorado, Arizona, California, and Texas) (Fig. 1 and Table 1).

We designated a neotype for *Pardosa sura* following the statements in the International Code of Zoological Nomenclature, based principally that it will clarify the taxonomic status of the species of interest; data and description are sufficient to ensure recognition of the specimen designated. Additionally, type specimens (holotype and lectotype) have been lost, though we made the necessary steps to trace them.

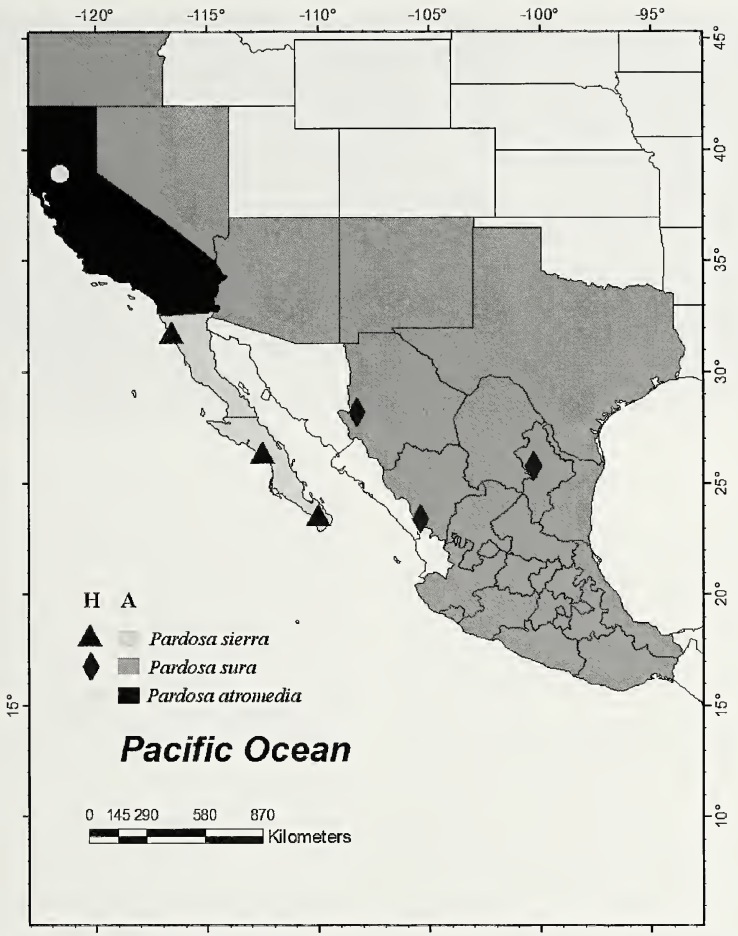

Figure 1.—Distribution of the *Pardosa sierra* species complex. Symbols represent haplotype origins (H); gray and black areas (A) represent potential distribution of the species based on location of specimens in collections. *P. sierra* = triangles and light gray; *P. atromedia* = circle and black area; *P. sura* = diamonds and dark gray.

Pardosa sierra Banks 1898
Figs. 1, 2, 5

Pardosa sierra Banks 1898:274; Petrunkevitch 1911:575; Gertsch, 1934:19; Roewer, 1954:194; Bonnet, 1958:3422; Barnes 1959:14; Vogel 2004:72; Platnick 2009.

Material examined.—Lectotype (present designation) female: MEXICO: *Baja California*: Sierra Laguna: 1898 (Nathan Banks Coll.), label does not show collection record (MCZ). Paralectotype male: MEXICO: *Baja California Sur*: collected from Sierra de la Laguna 2–4 November 2006 (M.M. Correa & C.Palacios) (CARCIB). Holotype female deposited in CAS was destroyed by the earthquake and fire of 1906.

Other material examined.—MEXICO: *Baja California*: Isla Cedros, 22 February 1945, 8♀ (B. F. Osorio & M. T. H. Tafall) (AMNH); Idem Gran Cañón, 10 March 1945, 6♀ (B.F. Osorio & M.T.H. Tafall) (AMNH); Tajo Branch of Cantil Canyon east side of Laguna Salada, 2♀ (T. Briggs) (CAS); Ensenada, April 2008, 3♂, 5♀ (García de León) (CARCIB); El Rosarito, April 2008, 1♂, 3♀ (García de León) (CARCIB); Arrollo Cataviña, 2♀ (CAS). *Baja California Sur*: Sierra la Laguna, 1898, 1♀; idem 2–4 November 2006, 50♂, 50♀ (M.M. Correa & C. Palacios) (CARCIB); San José de Comondú, 29 October

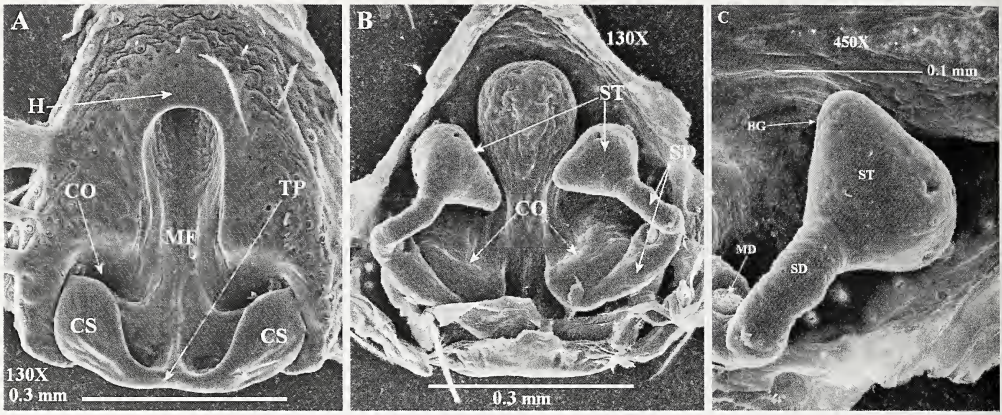

Figure 2.—A. Epigynum, ventral view of *Pardosa sierra* × 130. Scale = 0.3 mm. H, hood in anterior position; MF, middle field; CO, copulatory openings; TP, transverse piece; CS, crescent-shaped troughs. B. Epigynum, dorsal view × 130. Scale = 0.3 mm. ST, spermathecae; SD, copulatory ducts. C. Spermathecae, dorsal view × 450. Scale = 0.1 mm. BG, bulge of spermathecae; MD, microducts.

2006 (C. Palacios); 10♂, 15♀ (CARCIB); San Isidro - La Purísima, 28 October 2006, 5♂, 20♀ (C. Palacios); 5♂, 15♀ (CARCIB); San Pedro de la Presa, 19 June 2008, 50♂, 50♀ (M.M. Correa & C. Palacios) (CARCIB); Cadejé, 5 October 2006, 50♂, 50♀ (M.M. Correa & C. Palacios) (CARCIB); San Ignacio, 3 October 2006, 50♂, 50♀ (M.M. Correa & C. Palacios) (CARCIB); Mulegé, 4 October 2006, 50♂, 50♀ (M.M. Correa & C. Palacios) (CARCIB); El Chorrro Región del Cabo, 23 October 2005, 10♂, 20♀ (M.M. Correa & C. Palacios) (CARCIB).

Diagnosis.—Females of *Pardosa sierra* can be easily distinguished from other taxa in the *lapidicina* group by the crescent-shaped sclerites of the epigynum, which lie at the apical edge of the lateral expansions of the cavity, forming a sigmoid curve (Fig. 2 A). Copulatory ducts are straight and wider at their base, but never winding as in *P. atromedia*. In males, the embolus extends across the bulb, with the tip curving apically (Figs. 5 A, C) and ending in a tip differing from those presented in *P. atromedia* and *P. sura*. The terminal apophysis is shorter than the median apophysis, which is thumb-like and straight. *Pardosa sierra* differs from other closely related species on the basis of the following unique mtDNA nucleotide substitutions at the following reference alignment positions: C (51), G (54), G (63), G (102), T (264), G (267), G (279), T (226), G (390), C (477), A (480), C (489), G (543) and T (606).

Description.—*Female* (lectotype): Total length 5.8 mm, carapace length 2.75 mm, width 2.31 mm. Prosoma light brown, eye region black, an irregular broad band on each upper side, which indents in the middle area before the groove; clypeus with white and black hairs, large marginal spots and a patch across the clypeus. Sternum brownish black, covered with hairs, with pale margins. Chelicerae brown, with some dark hairs. Endites dusky brown with pale tips; labium dusky brown with a pale tip. Legs slender, hind pair very long; tibiae I and II with three subequal pairs of spines and a short pair on distal portion; color, light brown with black markings, consisting of wide annulling, two on femora, one on patellae, two bands on tibiae and a black spot on coxae, all trochanters notched, further shadings on underside of femora. Dorsal view of abdomen with blackish and light gray spots and specks, ventral side gray, more or less shaded with darker gray. Eyes of first row subequal, middle eyes rather farther apart than from lateral eyes. Transverse portion of epigynum occupies approximately one-half of total length (Fig. 2), with pair of crescent-shaped troughs on the floor on each side of the transverse portion. Middle field widened anteriorly, with narrowest portion in the middle 0.10 mm long (Fig. 2A). Length of transverse piece 0.39 mm, width 0.39 mm (Fig. 2A). Crescent-shaped troughs on each side of the transverse piece canal-like, taking form of sigmoid curve with wide and rounded borders that reduce middle area of transverse piece (Fig. 2A). In dorsal view, spermatic ducts straight at the base (attached to copulatory openings). Spermathecae semi-spherical, with prominent bulge on the retrolateral sides (Fig. 2C). As well as in the other species described here, the epigynum has a rounded structure located in the middle part of the spermatic ducts that appears to be a series of microducts (MD in Fig. 2C).

Male (Paralectotype): Total length 4.25 mm, carapace length 2.18 mm, width 1.76 mm. Color and body shape similar to female, but darker. Embolus short, with thin tip. Conductor of the male pedipalpal structure sword-shaped and projecting upward from the bulb. This process is sufficiently sclerotized and conspicuous to be distinctly visible in the unexpanded pedipalp. Conductor rounded. Median accessory process (Fig. 5A) much less conspicuous and concealed or partially concealed by the conductor in unexpanded pedipalp.

Variations.—Females have average body length of 7.87 ± 0.52 mm, carapace length averaging 2.96 ± 0.25 mm, width 2.52 ± 0.21 mm. Epigyna vary as follows: MF with average length of 0.12 ± 0.02 mm; EpL 0.39 ± 0.06 mm and EpW 0.39

Table 2.—Measurements (mm) of female of *Pardosa* species.

	Pardosa sierra $n = 10$		*Pardosa atromedia* $n = 10$		*Pardosa sura* $n = 10$	
	Mean ± SD	Min – Max	Mean ± SD	Min – Max	Mean ± SD	Min – Max
Total Length	7.87 ± 0.52	7.08–8.63	6.81 ± 0.64	6.00–7.50	7.22 ± 0.77	5.58–8.25
Carapace Length	2.96 ± 0.25	2.48–3.25	2.93 ± 0.19	2.48–3.25	3.04 ± 0.33	2.58–3.55
Carapace Width	2.52 ± 0.21	2.24–2.85	2.51 ± 0.17	2.27–2.90	2.56 ± 0.34	2.09–3.15
WE	1.43 ± 0.10	1.29–1.57	1.42 ± 0.09	1.27–1.57	1.40 ± 0.12	1.14–1.61
LE	1.57 ± 0.11	1.33–1.69	1.55 ± 0.09	1.37–1.71	1.53 ± 0.13	1.27–1.76
PMEW	0.96 ± 0.04	0.86–1.02	1.00 ± 0.08	0.86–1.10	1.05 ± 0.10	0.88–1.18
PLEW	1.29 ± 0.08	1.14–1.39	1.36 ± 0.10	1.18–1.47	1.39 ± 0.14	1.18–1.59
POQ Length	0.96 ± 0.06	0.84–1.06	1.00 ± 0.08	0.86–1.12	1.05 ± 0.10	0.90–1.18
Femur I	2.93 ± 0.24	2.50–3.30	3.00 ± 0.16	2.70–3.20	2.80 ± 3.20	2.21–0.34
Femur II	2.89 ± 0.28	2.45–3.35	2.95 ± 0.15	2.65–3.15	2.74 ± 0.33	2.18–3.15
Tibia I	2.59 ± 0.22	2.20–2.90	2.69 ± 0.18	2.40–2.90	2.51 ± 3.35	1.82–0.44
Tibia III	2.30 ± 0.18	2.00–2.55	2.45 ± 0.14	2.20–2.60	2.51 ± 0.25	2.27–3.10
Tarsus I	1.15 ± 0.07	1.04–1.24	1.15 ± 0.06	1.02–1.24	1.07 ± 0.10	0.90–1.29
Trochanter IV	0.52 ± 0.04	0.49–0.59	0.58 ± 0.03	0.53–0.63	0.55 ± 0.07	0.45–0.65
EpL	0.39 ± 0.06	0.33–0.55	0.51 ± 0.04	0.41–0.55	0.50 ± 0.07	0.39–0.61
EpW	0.39 ± 0.03	0.33–0.47	0.49 ± 0.04	0.43–0.53	0.47 ± 0.55	0.41–0.04
MF	0.12 ± 0.02	0.10–0.16	0.13 ± 0.01	0.12–0.16	0.14 ± 0.03	0.10–0.18

± 0.03 mm. Troughs of epigynum vary in degree of sclerotization and sometimes obscure or transparent. Males have average body length of 4.72 ± 0.32 mm, carapace length averages 2.40 ± 0.14 mm, width 1.97 ± 0.13 mm, pedipalpal structures vary in some measurements as follows: TP averages 0.50 ± 0.06 mm, FP 0.87 ± 1.02 mm, BT 0.80 ± 0.07 mm. (Tables 2, 3). Range of body coloration from pale yellow to dusky brown in females; males darker than females, principally in ocular area.

Distribution and Natural History.—*Pardosa sierra* occurs in most parts of the Baja California Peninsula and is presumably endemic to this region (Fig. 1). The habitat preference of this species is similar to other species in the *lapidicina* group. It prefers the edge of rivers and oases or natural and artificial rocky wetlands, where it is often collected by hand and/or with the use of pitfall traps.

Pardosa atromedia Banks 1904
Figs. 1, 3, 6

Pardosa atromedia Banks 1904:355; Petrunkevitch 1911:571 (in part); Roewer 1954:194 (junior synonymy of *P. sierra* Banks 1898).

Pardosa sierra Banks 1898: Barnes 1959:14.

Material examined.—Lectotype (present designation) female: USA: *California*: Curtice, 1904 (Nathan Banks Coll.), label does not show collection data (MCZ). Paralectotype male: USA: *California*: Los Angeles Co., Fish Canyon, San Gabriel Mountains, 2 February 1950, 1♂ (E.I. Schlinger)

Table 3.—Measurements (mm) of male of *Pardosa* species.

	Pardosa sierra $n = 10$		*Pardosa atromedia* $n = 10$		*Pardosa sura* $n = 10$	
	Mean ± SD	Min–Max	Mean ± SD	Min–Max	Mean ± SD	Min–Max
Total Length	4.72 ± 0.32	4.25–5.33	5.57 ± 0.22	5.33–5.83	4.91 ± 0.51	4.35–5.50
Carapace Length	2.40 ± 0.14	2.18–2.64	2.62 ± 0.22	2.30–2.88	2.50 ± 0.19	2.33–2.73
Carapace Width	1.97 ± 0.13	1.76–2.18	2.21 ± 0.14	2.09–2.36	2.04 ± 0.20	1.82–2.27
WE	1.15 ± 0.08	1.04–1.24	1.19 ± 0.07	1.12–1.27	1.11 ± 0.08	1.02–1.22
LE	1.26 ± 0.07	1.18–1.37	1.36 ± 0.03	1.31–1.39	1.31 ± 0.11	1.18–1.47
PMEW	0.80 ± 0.03	0.75–0.86	0.97 ± 0.03	0.94–1.02	0.86 ± 0.05	0.80–0.94
PLEW	1.06 ± 0.05	0.94–1.14	1.25 ± 0.06	1.18–1.33	1.17 ± 0.07	1.08–1.24
POQ	0.78 ± 0.03	0.75–0.84	0.94 ± 0.01	0.92–0.94	0.85 ± 0.06	0.80–0.94
Femur I	2.20 ± 0.18	1.91–2.52	2.73 ± 0.20	2.55–3.00	2.37 ± 0.25	2.10–2.70
Femur II	2.14 ± 0.16	1.85–2.45	2.67 ± 0.17	2.50–2.85	2.31 ± 0.23	2.05–2.60
Tibia I	2.22 ± 3.20	1.76–0.48	2.55 ± 0.38	2.05–3.10	2.14 ± 0.19	2.00–2.45
Tibia III	2.13 ± 0.47	1.57–2.80	2.41 ± 0.23	2.15–2.75	1.95 ± 0.19	1.80–2.25
Tarsus I	0.95 ± 0.03	0.90–1.00	1.10 ± 0.04	1.06–1.14	0.99 ± 0.09	0.86–1.12
Trochanter IV	0.41 ± 0.03	0.37–0.45	0.49 ± 0.00	0.49–0.49	0.44 ± 0.05	0.39–0.49
TP	0.50 ± 0.06	0.41–0.63	0.59 ± 0.02	0.57–0.63	0.57 ± 0.06	0.49–0.65
FP	0.87 ± 1.02	0.82–0.06	0.99 ± 0.06	0.92–1.06	0.94 ± 0.11	0.82–1.08
BT	0.80 ± 0.07	0.73–0.94	0.99 ± 0.05	0.94–1.06	0.86 ± 0.05	0.82–0.94
Bx	0.48 ± 0.07	0.41–0.65	0.60 ± 0.02	0.59–0.63	0.53 ± 0.04	0.49–0.59
AB	0.33 ± 0.02	0.29–0.37	0.39 ± 0.04	0.35–0.43	0.33 ± 0.02	0.29–0.35

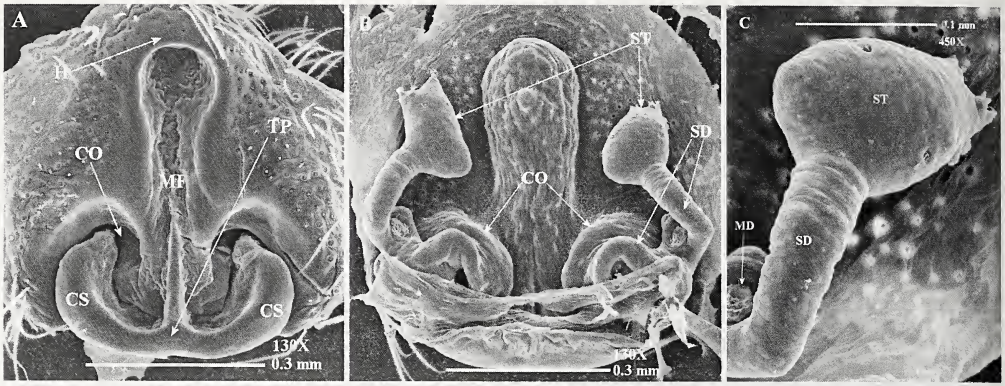

Figure 3.—A. Epigynum, ventral view of *P. atromedia* × 130. Scale = 0.3 mm. H, hood in anterior position; MF, middle field; CO, copulatory openings; TP, transverse piece; CS, crescent-shaped troughs. B. Epigynum dorsal view × 130. Scale = 0.3 mm. ST, spermathecae; SD, copulatory ducts. C. Spermathecae, dorsal view × 450. Scale = 0.1 mm. BG, bulge of spermathecae; MD, microducts.

(AMNH). Holotype female deposited in CAS was destroyed by the earthquake and fire of 1906.

Other material examined.—USA: *California*: Curtice, 1904, 1♀ (Nathan Banks Coll.) (MCZ); 40°N, 111°W (AMNH); Calaveras Co., 5 mi west of Durrington, Stanislaus River, 5 August 1953, 2♀ (W. Gertsch & J. Gertsch) (AMNH); Toulumne Co., Pinecrest, 6 July 1947, 1♀ (P. H.Arnaud) (CAS); Contra Costa Co., Diablo, 25 March 1947, 6♀ (B. Malkin & D.G. Kelley) (AMNH); Monrovia Canyon, 26 July 1931, 34°10′N, 117°5′W, 2♀ (Chamberlin & Ivie) (AMNH); San Diego River near mouth, 12 July 1931, 32° 46′N, 117°10′W, 1♀ (Chamberlin & Ivie) (AMNH); San Diego Co., Indian Canyon, 25 May 1948, 1♂, 1♀ (M.A. Pearce) (AMNH); Siskiyou Co., Wildcat Creek, 1 mi NW Callahan, 31 July 1968, 1♀ (H.B. Leech) (CAS); San Juan Creek, near mountains, 18 July 1931, 33°27′N, 117°40′W, 2♀ (Chamberlin & Ivie) (AMNH); Palm Springs, 5 April 1925, 33° 55′N, 116° 40′W, 2♀ (Chamberlin & Ivie) (AMNH); San Diego, 2♀; Lower End Indian Canyon, 14 July 1948, 1♀ (M.A. Pearce) (AMNH); Santiago, 33°45′N, 117°45′W, 29 December 1930, 1♀ (Chamberlin & Ivie) (AMNH); Los Angeles Co., Valyermo, Los Angeles Big Rock Creek, 4200 ft, 12 June 1943, 1♀ (K. Cowles) (AMNH); Mono Co., Montgomery Canyon, 13 July 1941, 5♀ (M.A. Pearce) (AMNH); Los Angeles Co., Fish Canyon, San Gabriel Mountains, 2 February 1950, 1♂ (E.I. Schlinger) (AMNH), Idem, Los Angeles Co., 2 October 1944, 1♀ (E.I. Schlinger) (AMNH); Idem, Los Angeles Co., 29 April 1945, 3♂, 5♀ (E. I. Schlinger) (AMNH); Roads End, Kern River, 3 July 1956, 2♀ (V. Roth & W. Gertsch) (AMNH); Claremont, California (R.V.C.) (R-4) 1♀ (Chamberlin) (AMNH); Idem 34°3′N, 117°48′W, 1♀ (Chamberlin); Yosemite Park (Wawona Camp), 17 September 1941, 37°32′N, 119°39′W, 1♂ (Ivie) (AMNH); Mariposa Co., Idem, 14 July 1952, 1♂, 3♀ (W. Gertsch, Schrammel & M. Cazier) (AMNH); Irvins, near Santa Ana Park, 17 July 1931, 33°40′N, 117°48′W, 1♂ (Chamberlin & Ivie) (AMNH); Near San Diego Mission, 12 July 1931, 5♀ (Chamberlin Det. Ivie) (AMNH); San Diego, 2 June 1948, 2♂, 3♀ (M.A. Pearce) (AMNH); Eatons Canyon, March 1913, Quad. 34°N, 118°W, 2♂ (Chamberlin) (AMNH); Idem, March 1913, Quad. 34°N, 118°W, 2♂ (Chamberlin) (AMNH); Inyo Co., Olancha, 18 July 1952, 1♀ (W. Gertsch, Schrammel & M. Cazier) (AMNH); San Juan Hot Spring, 3 July 1931, 33°36′N, 117°33′W, 2♀ (Chamberlin & Ivie) (AMNH); Idem, 3 July 1931, 33°36′N, 117°33′W, 4♀ (Chamberlin & Ivie) (AMNH); Santa Monica, 12♀ (Det. Gertsch) (AMNH); Idem, 9♀ (Det. Gertsch) (AMNH); San Diego Co., Houser Creek, 29 June 1948, 4♀ (M.A. Pearce) (AMNH); Pine Forest, 21 November1927, 1♀ (W.G. Dietz); Riverside Co., Magnesia Canyon, 21 April 1951, 1♀ (E.I. Schlinger) (AMNH); Riverside Co., Idyllwild, 7 July 1953, 1♀ (W. Gertsch & J. Gertsch) (AMNH); Palm Spring, Andreas Canyon, 3 March 1956, 3♂, 5♀ (V. Roth) (AMNH); San Diego Co., Boulder Creek, 6 May 1948, 1♂, 8♀ (M.A. Pearce) (AMNH); Tulare Co., Kawea River, 5 mi E. Treerivers, 1258 ft17 July 1952, 2♀ (W. Gertsch) (AMNH); Los Angeles Co., Tanbark Flats, San Gabriel Mountains, 20 June 1952, 1♂, 6♀ (W. Gertsch) (AMNH).

Diagnosis.—Females of *Pardosa atromedia* can be differentiated from *P. sierra* and *P. sura* by the crescent-shaped sclerites of the epigynum which are curved and slender, almost with the same thickness as in the apical lateral parts and in the middle part of the transverse piece (Fig. 3A). The thin septal ridge extends apically to the hood. Copulatory ducts winding at their base and never are straight as in *P. sierra* and *P. sura*. In males, the embolus extends across the bulb with the tip curving apically, but ends in a blunt tip (Fig. 6C), not as in *P. sierra*. The terminal apophysis is nearly half as long as the median apophysis. It is thumb-like and straight; the median accessory process is indistinguishable with respect to *P. sierra* and *P. sura*. *Pardosa atromedia* differs from other closely related species on the basis of the following unique mtDNA nucleotide substitutions at the following reference alignment positions: C (42), G (66), A (81), G (114), G (129), G (288) and A (423).

Description.—*Female* (Lectotype): Total length 7.03 mm., width 2.39 mm. Cephalothorax pale yellow with median band

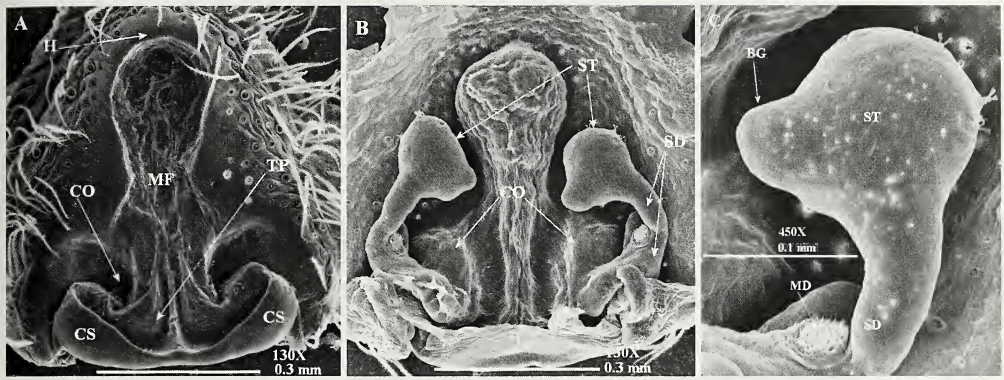

Figure 4.—A. Epigynum, ventral view of *P. sura* × 130. Scale = 0.3 mm. H, hood in anterior position; MF, middle field; CO, copulatory openings; TP, transverse piece; CS, crescent-shaped troughs. B. Epigynum dorsal view × 130. Scale = 0.3 mm. ST, spermathecae; SD, copulatory ducts. C. spermathecae dorsal view × 450. Scale = 0.1 mm. BG, Bulge of spermathecae; MD, microducts.

light brown, eye region black, irregular broad band on each upper side, which indents in the middle area before the groove; clypeus with white and black hairs, large marginal spots and patch across it. Sternum brown, covered with hairs, with pale margins. Chelicerae light reddish to dark brown, shaded with dusky brown. Endites brown with pale tips, labium brown with pale tip. Legs slender, hind pair very long; tibiae I and II with 4 pair of subequal spines, legs pale yellowish with dusky brown markings, consisting of wide annulling, two on femora, one on patellae, two bands on tibiae and a black spot in coxae, further shadings underside of the femora. Dorsal view of abdomen marked with gray and light yellow spots and specks; ventral side light gray, more or less shaded with darker gray. Eyes of first row subequal, middle eyes rather farther apart than from lateral eyes. Transverse piece of epigynum 0.55 mm. wide, 0.53 mm long (Fig. 3A). Crescent-shaped troughs on each side of transverse piece curved and slender, with almost equally thick in middle part of transverse piece. In dorsal view, spermatic ducts winding at base and straight at anterior part, with same thickness (Fig. 3B). Spermathecae almost spherical, with apical small bulges (Fig. 3C).

Male (Paralectotype): Total length 5.83 mm, carapace length 2.88 mm, width 2.09 mm. Appearance similar to female. Conductor of the male pedipalp sword shaped and projecting upward from the bulb, conductor truncated, embolus little winding with blunt tip, median accessory process, median and terminal apophysis similar to those presented in *P. sierra* and *P. sura*.

Variation.—Females have average body length of 6.81± 0.64 mm, carapace length averages 2.93 ± 0.19 mm, width 2.51 ± 0.17 mm; epigynum varying as follows: MF with average length of 0.13 ± 0.01 mm; EpL 0.51 ± 0.04 mm and EpW 0.49 ± 0.04 mm. Troughs of epigynum vary in degree of sclerotization and sometimes obscure or transparent. Males have average body length of 5.57 ± 0.22 mm, carapace length averages 2.62 ± 0.22 mm, width 2.21 ± 0.14 mm, pedipalps vary in some measurements as follows: average TP of 0.59 ± 0.02 mm, FP 0.99 ± 0.06 mm, BT 0.99 ± 0.05 mm. Body color ranges from pale yellow to dusky brown in females and sometimes reddish; males darker than females, principally in ocular area.

Distribution and Natural History.—*Pardosa atromedia* occurs in major parts of California and apparently is restricted to the state (Fig. 1). The habitat preference of this species is similar to other species in the *lapidicina* group. It prefers the edge of rivers, generally with rocks, where it is often collected by hand.

Pardosa sura Chamberlin & Ivie 1941
Figs. 1, 4, 7

Pardosa sura Chamberlin & Ivie 1941:10; Roewer 1954:194.
Pardosa sierra Banks 1898: Barnes 1959:14.

Material examined.—Neotype, (present designation) female: USA: *California*: West Sierra County, Sierra City, 7 mi, 8 July 1952 (W. Gertsch) (AMNH). Paratype male: USA: *Utah:* Beaver Canyon, 6 August 1927 (R.V. Chamberlin & W. Ivie) (AMNH). Holotype female and paratype female deposited in Museum of Natural History at the University of Utah, are lost; the arachnological collection of this institution has changed its location several times until finally it was integrated into the collection of the AMNH, but we did not find these specimens in that collection.

Other material examined.—USA: *Oregon*: Corvallis, Kiger Isl., on rocky shore, 18 July 1951, 1♂ (V.Roth) (AMNH); Robinette, 18 June 1938, 1♀ (Hatch) (CAS). *Utah:* Beaver Canyon, 6 August 1927, 5♂, 5♀ (R.V. Chamberlin & W. Ivie) (AMNH). *California*: West Sierra County, Sierra City, 7 mi, 8 July 1952, 2♀ (W. Gertsch) (AMNH). *Arizona*: Sabino Canyon Sta., Catalina Mountains, 26 July 1948, 2♀ (W. Gertsch & J. Gertsch) (AMNH); Roosevelt Lake, 23 August 1923, 1♀ (R. Flock) (CAS); Grand Canyon, Indian Gardens, 24 July1934, F340724, 1♂, 1♀ (Lutz Det. Gertsch) (AMNH); Coyote Mountains, 4–7 August 1916, 1♂, 1♀ (Lutz Det. Gertsch) (AMNH); 5 mi west Portal, Southwestern Research Station, 6–20 July 1955, 2♀ (W. Gertsch) (AMNH); Oak Creek Canyon, Manzanita Camp, 26 July 1950, 2♀ (M. A. Cazier)

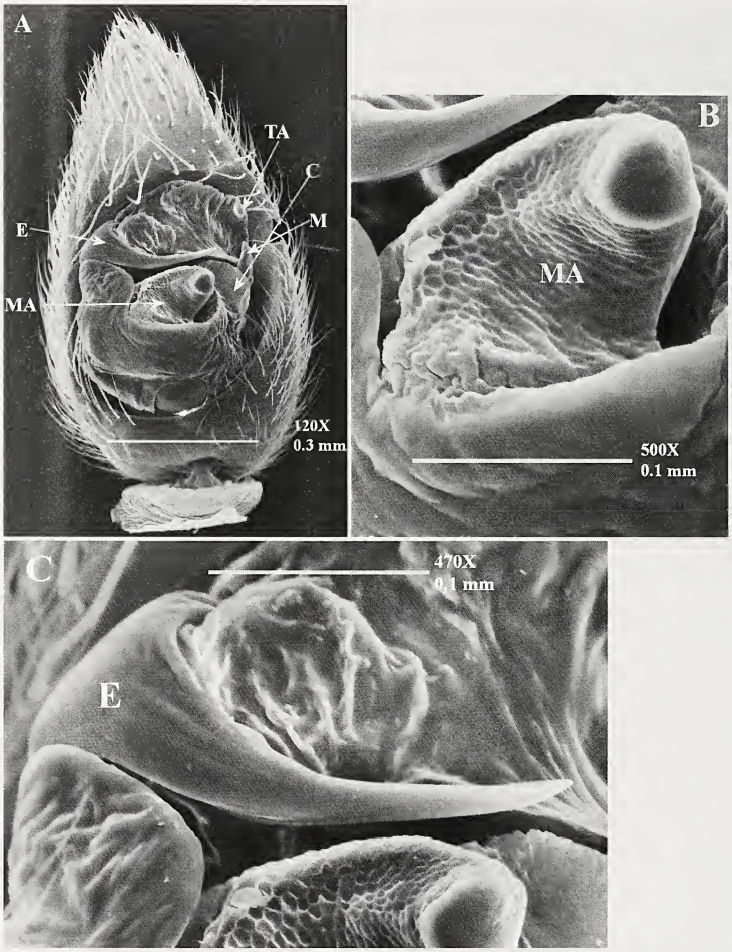

Figure 5.—A. Male pedipalpal ventral view of *Pardosa sierra* × 120. Scale = 0.3 mm. E, embolus; MA, median apophysis; TA, terminal apophysis; M, median accessory process; C, conductor. B. Close-up median apophysis × 500. Scale = 0.1 mm. C. Close-up embolus × 470. Scale = 0.1 mm.

(AMNH); Huachuca Mts., Carr Canyon, 5000 ft, 1 August 1952, 2♀ (W. Gertsch, Schrammel & M. Cazier) (AMNH); Cochise Co., Chiricahua Mountains, Cave Creek, 5500 ft., 16 June 1958, 1♀ (MacNeill) (CAS); Moenocupi, 24 July 1952, 1♀ (W. Gertsch, Schrammel & M. Cazier) (AMNH); Chiricahua National Monument, 15 July 1948, 3♀ (C. Vauries & P. Vauries) (AMNH) Catalina Mountains, 10 mi S Oracle Station, 25 July 1949 (W. Gertsch & J. Gertsch) (AMNH); Huachuca Mts., Carr Canyon, 5000 ft, 3 June 1952, 15♀ (W. Gertsch, Schrammel & M. Cazier) (AMNH); Bottom Walnut Canyon, 18 August 1934, 1♀ F340818 (Lutz Det. Gertsch) (AMNH); 5 mi W Portal, Southwestern Research Station, 15 June 1955, 1♂, 1♀ (M. Statham) (AMNH); Oak Creek Canyon, Manzanita Camp, 27 July 1950, 2♂, 5♀ (M. A. Cazier) (AMNH); Graham Mountains near Safford, 14 July 1955, 2♀ (V. Roth & W. Gertsch) (AMNH); Oak Creek Canyon, 22 July 1949, 3♀ (W. Gertsch & J. Gertsch) (AMNH); White River, 9 July 1940, 3♀ (Gertsch & Hook) (AMNH); Baboquivari Mts., Browns Canyon, 29–30 June 1952, 3♂ (H. B. Leech & J. W. Green) (CAS); Strawberry, 15 May 1939, 2♀ (R. H. Crandall) (AMNH); Tucson, Sabino Canyon, 5 June 1952, 1♂, 2♀ (W. Gertsch, Schrammel & M. Cazier) (AMNH);

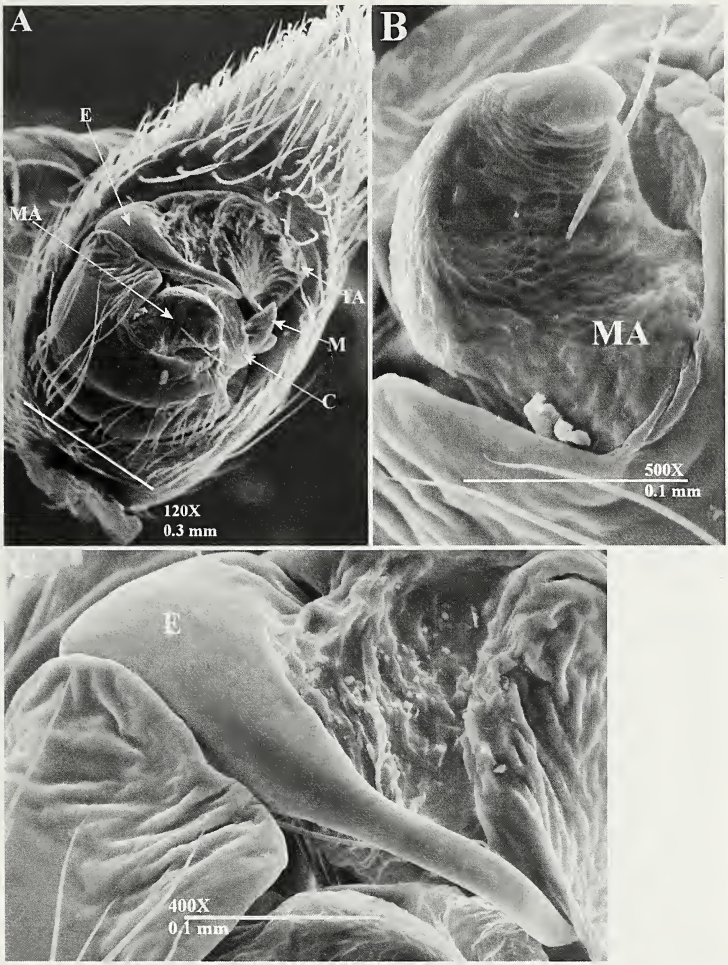

Figure 6.—A. Male pedipalpal ventral view of *Pardosa atromedia* × 120. Scale = 0.3 mm. E, embolus; MA, median apophysis; TA, terminal apophysis; M, median accessory process; C, conductor. B. Close-up median apophysis × 500. Scale = 0.1 mm. C. Close-up embolus × 400. Scale = 0.1 mm.

10 mi NE White River, 8–11 July 1940, 1♂, 3♀ (Gertsch & Hook) (AMNH); Miami, 12 May 1938, 1♀ (R. H. Crandall) (AMNH). *Texas*: Sanderson, 26 May 1952, 1♀ (W. Gertsch, Schrammel & M. Cazier) (AMNH). *Idaho*: 10 mi S Swan Valley town, 6 July 1935 (W. Ivie) (AMNH). *Colorado*: Montrose, near Water, 25 July 1941 1♀ (C. Goodnight & M. Goodnight). MEXICO: *Chihuahua*: San Francisco Mesa near Santa Barbara, 8 July 1948, 1H (W. Gertsch) (AMNH); 44 mi N Chihuahua, 13 June 1939, 1♂, 1♀ (A.M. & L.I. Davis) (AMNH); Cañón Prieto near Primavera, 30 June 1947, 1♀ (W. Gertsch) (AMNH); Puente Bravo, 9 October 2007, 2♀ (M.M Correa & F. J. García de León) (CARCIB); Cerocahui, 25–26 June 1979, 2♀ (G. J. Millick) (CAS). *Coahuila*: 5 mi W Saltillo, 5 July 1936, 2♂ 3♀ (L.I. Davis) (AMNH). *Nuevo León*: Monterrey, 23 May 1952, 1♂, 1♀ (W. Gertsch, Schrammel & M. Cazier) (AMNH); 25 mi W of Monterrey, 6 July 1936, 1♂, 1♀ (L.I. Davis) (AMNH); Chipinque, 15 July1942, 1♂, 1♀ (Bonet, Osorio & Pelaez) (AMNH); Montemorelos, 23 May 1952, 1♂, 1♀ (W. Gertsch) (AMNH). *Tamaulipas*: Victoria, 12 June 1936, 1♂, 2♀ (L.I. Davis) (AMNH). *Durango*: 10 mi E El

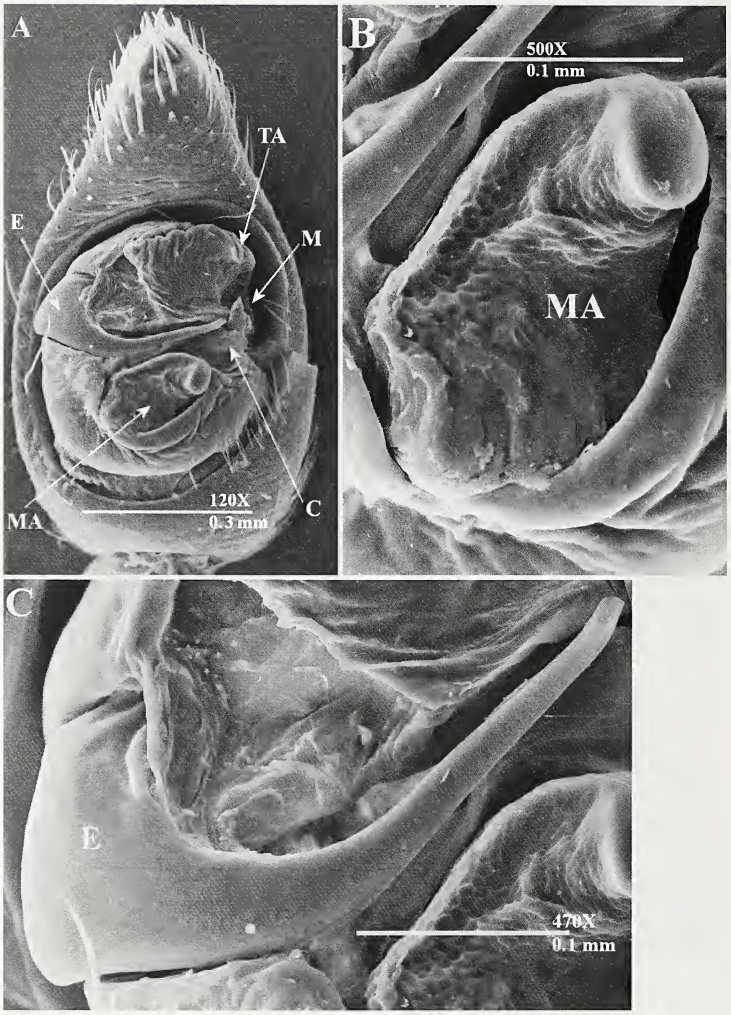

Figure 7.—A. Male pedipalpal ventral view of *Pardosa sura* × 120. Scale = 0.3 mm: E, embolus; MA, median apophysis; TA, terminal apophysis; M, median accessory process; C, conductor. B. Close-up median apophysis × 500. Scale = 0.1 mm. C. Close-up embolus × 470. Scale = 0.1 mm.

Salto, 8 August 1947, 4♀ (W. Gertsch) (AMNH); Palos Colorados, 5 August 1947, 1♂, 3♀ (W. Gertsch) (AMNH). *San Luis Potosí*: Picolo, 21 May 1952, 2♂, 12♀ (W. Gertsch, Schrammel & M. Cazier) (AMNH). *Hidalgo*: 5 mi S Zimapan, 20 July 1956, 2♀ (V. Roth & W. Gertsch) (AMNH); Ixmiquilpan, 6 July 1944, 1♀ (L.I. Davis) (AMNH); 10–25 mi S of Jacala, 20 July 1956, 1♀ (V. Roth & W. Gertsch) (AMNH). *Distrito Federal*: Almoloya del Rio, 7 April 1944, 1♂, 1♀ (Hernandez & Mercado) (AMNH). *Jalisco*: Chapala, 22 June 1941, 2♀ (A.M. Davis) (AMNH). *Michoacán*: 10 mi W Tizapán, 11 July 1972, 1♀ (A.R. Brady & A. Jung) (AMNH). *Morelos*: Cuernavaca, October 1944, 1♀ (N.L.H. Krauss) (AMNH). *Puebla*: Tehuacán, 24 July 1956, 7♀ (V. Roth & W. Gertsch) (AMNH). *Gerrero*: Ixtapan de la Sal, 21–28 August 1946, 2♀ (H. Wagner) (AMNH). *Oaxaca*: near Oaxaca, 12 April 1941, 1♀ (H. Wagner) (AMNH); Base San Felipe

Mountains, 16–17 September 1947, 2♀ (B. Malkin) (AMNH). *Veracruz*: Cordava 492, 1♀(AMNH).

Diagnosis.—Females of *Pardosa sura* differ from *P. sierra* and *P. atromedia* by the crescent-shaped sclerites of the epigynum that are canal-like in shape with the apical edge of the lateral crescent sclerites of the cavity forming an angle of 45°. The thin septal ridge extends apically to the hood. Copulatory ducts are straight at their base and never winding as in *P. atromedia*, subequal in thickness, and not wider at their base as in *P. sierra*. In males, the pedipalpal structure has a long and thin embolus, which extends across the bulb with a curved and truncated tip that turns toward of the conductor; the base is wider than in *P. sierra* and *P. atromedia*. The conductor is short and truncated and opposite the embolus (Fig. 7C). *Pardosa sura* differs from other closely related species by the unique mtDNA nucleotide substitutions at the following reference alignment positions: G/A (18), G (57), C (72), G (78), T (114), T (129), G (216), G (237), G (249), A/G (291), G (303), A (333), G (336), G (342), T (387), G (399), T (426) and C (613).

Description.—*Female* (Neotype): Total length 8.25 mm, carapace length 3.55 mm, width 3.15 mm. Prosoma dusky brown; eye region black, irregular broad band on each upper side, which indents in the middle area before the groove; clypeus with white and black hairs, large marginal spots with patch across it. Sternum brownish-black, covered with hairs, with pale margins. Chelicerae dark brown, shaded with dusky brown. Endites and labium brown with pale tips. Legs slender, hind pair very long; tibiae I and II with 3 subequal spines and pair of short spines on distal part, legs dark brown with black markings, consisting of wide annulling. Dorsal side of abdomen marked with blackish and gray spots and specks; ventral side gray, more or less shaded with darker gray. Eyes of first row subequal, middle eyes rather farther apart than from lateral eyes. Transverse portion of epigynum occupies approximately one-half the total length (Fig. 4). Middle field of epigynum widened anteriorly, with narrowest portion in middle averaging 0.14 mm. (Fig. 4A). Transverse piece 0.47 mm long (Fig. 4A). Crescent-shaped troughs on each side of transverse piece also canal-like, but narrower with borders almost straight in 45° angle that reduces thickness in the middle area of transverse piece. In dorsal view, ducts have same thickness along it (Fig. 4B). Bulge of spermathecae stretched at base (Fig. 4C). In ventral view, epigynum has rounded structure in middle part of spermatic ducts that appears to be a series of microducts (MD in Fig. 4C).

Male (Paratype): Total length 4.35 mm, carapace length 2.33 mm, width 1.82 mm. Coloration and body shape as female. Male pedipalpal organ with small and truncated conductor, similar to that of *P. atromedia*. Embolus long and thin, extending across the bulb with curved and truncated tip; median accessory process, median and terminal apophysis very similar to *P. sierra* and *P. atromedia* (Fig. 7).

Variation.—Females with average body length of 7.22 ± 0.77 mm, carapace length averages 3.04 ± 0.33 mm; epigynum with variation as follows: MF with average length of 0.14 ± 0.1 mm; EpL 0.50 ± 0.07 mm and EpW 0.47 ± 0.55 mm. Troughs of epigynum vary in degree of sclerotization; sometimes obscure or transparent. Males with average body length of 4.91± 0.51 mm, carapace length averages 2.50 ± 0.19 mm, width 2.04 ± 0.20 mm, male pedipalps vary in some measurements as follows: TP averages 0.57 ± 0.06 mm, FP 0.94 ± 0.11 mm, BT 0.86 ± 0.05 mm. Body coloration ranges from pale yellow to reddish-brown in females. Males darker than females, principally in ocular area.

Table 4.—Pairwise *p*-distance values (in percent) for each category: median inter-quartile range and the smallest and largest observations compared with the median and standard deviation.

	Distances between species category (%)	Distances within species category (%)
Median	7.29 (6.18)	0.63 (0.16)
Min–Max	2.46–8.15	0.0–2.06
Mean	7.29 (0.70)	0.65 (0.35)

Distribution and Natural History.—*Pardosa sura* occurs from Oregon, northeastern parts of California, Utah, Colorado, Arizona, and Texas in USA; in Mexico from Chihuahua to Veracruz. It is not found or reported from Sonora, Sinaloa, or Baja California Peninsula in Mexico (Fig. 1). Habitat preferences of this species are similar to other species in the *lapidicina* group. It prefers the edge of rivers, generally with rocks, where it is often collected by hand.

General Remarks.—Twenty specimens per taxon were measured (females $n = 10$ and males $n = 10$) and analyzed. The somatic characteristics (Tables 2 and 3) show that in both sexes the different somatic parts measured are useless as a means to distinguish among species, because in most parameters a prominent area of overlap exists. *P. sura* shows the largest variation in all measurements, covering the range ($P > 0.05$) of the other two species (Tables 2, 3). Genitalia differ among females. Male pedipalpal structure, especially that of the pedipalpal bulb, is similar from species to species (Table 3); differences among males lie in the shape of the median apophysis, terminal apophysis, and embolus (Figs. 5B, 6B, 7B), which vary slightly. The median accessory process does not appear to vary among species.

Molecular data.—The average nucleotide composition in these three species of *Pardosa* (*P. sierra*, *P. atromedia*, and *P. sura*) and other species (including the *lapidicina* group) indicates that the nucleotide composition among *Pardosa* species is homogeneous (data not shown). The data included 548 invariant sites and 82 variable sites (consisting of 75 parsimony-informative sites and seven singleton sites). As observed in other spiders (Astrin et al. 2006), there is an A+T bias in the third codon position (data not shown) of the *lapidicina* group of *Pardosa* COI.

The Shapiro-Wilk test rejected the hypothesis of normal distribution of distance for this molecular marker. Distances between individuals were arranged in two categories: intra-species and interspecies. We did not encounter haplotype-sharing among taxa. Genetic divergence (measured by *p*-distances) for any species ranging from 0.16 to 1% were less than those between individuals of different species, ranging from 2.46 to 6.9% (Tables 4, 5). The largest divergences were observed in comparisons involving *P. astrigera*, which was chosen because it represents the major haplotype collection of a species in the genus *Pardosa*, where the differences were higher (Table 4, Fig. 8).

Table 5.—Distance matrix (*p*-distance or uncorrected) among *Pardosa* species category; distances within species category in diagonal.

	Species	1	2	3	4	5	6	7
1	*P. valens*	0.0032						
2	*P. steva*	0.0246	0.0016					
3	*P. vadosa*	0.0571	0.0500	0.0032				
4	*P. sura*	0.0397	0.0405	0.0593	0.0016			
5	*P. atromedia*	0.0635	0.0516	0.0683	0.0582	0.0032		
6	*P. sierra*	0.0643	0.0571	0.0659	0.0526	0.0690	0.0016	
7	*P. astrigera*	0.0766	0.0655	0.0719	0.0815	0.0733	0.0738	0.0065

Using *p*-distance data, we found that these lycosid spiders have a between-species genetic divergence from 2.46–6.90% with respect to the *lapidicina* group and within-species from 0.0–2.06% in this fragment of the COI gene (Table 5). The gap range was +0.4, indicating no overlap between categories (intraspecific vs. interspecific). Additionally, box-and-whisker plots appear suited for DNA taxonomy for interspecific purposes because they displayed variations simultaneously at intraspecific and interspecific levels (Fig. 8).

Finally, the topology of the COI NJ species identification tree (Fig. 9) showed that morphological conspecifics grouped together whereas between species, obvious segregation could be discerned (Fig. 9; see Table 5 for quantitative results).

Splits within species were slight (Fig. 9, Table 4) in all cases, but conspicuous among species (Fig. 9, Table 5). This is in contrast to the absence of detectable morphological variation in somatic characteristics and the slight differences in male but marked differences in female genitalia.

DISCUSSION

The morphological differences in females of the *P. sierra* complex are more conspicuous than those of the males. This situation probably led Barnes (1959) to synonymize *P. atromedia* and *P. sura* with *P. sierra*. Nevertheless, he identified differences between females of *P. sierra* and *P. sura*, but probably did not find differences between *P. atromedia* and *P. sura*, registering just two morphs of "*P. sierra*."

These three genitalic morphs have conspicuously distinct characteristics that can be used for taxonomic purposes, such as the shape of transverse piece, the spermatic conduct, and spermathecae in females and conductor, embolus, median apophysis, terminal apophysis, and median accessory process in males. These genital structures provide sufficient evidence to suggest that these morphological variations correspond to interspecific differentiation, as reported for other species (Dondale & Redner 1984; Chang et al. 2007; Wiemers & Fiedler 2007; Dreyer & Brady 2008).

Because the type material of *P. sura* was lost, a neotype was designated. The original material consisted of one holotype and one paratype deposited in the Utah Museum of Natural History (Chamberlin & Ivie 1941), which was later transferred to the American Museum of Natural History. This material was not found when we checked the specimens in the AMNH collection.

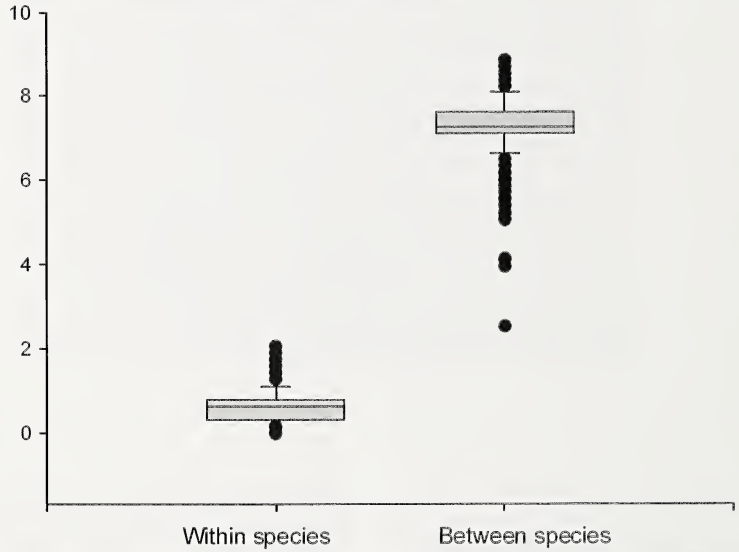

Figure 8.—Box plots of *p*-distances for a fragment of COI. Boxes indicate inter-quartile range (IQR: between upper [Q3] and lower [Q1] quartile). Black bar designates median, whiskers indicate values within 1.5× the IQR beneath Q1 or 1.5× above Q3. 'Mild' outliers (circles): between 1.5× and 3× IQR. Total of 2,216 pair wise comparisons for within-species category and total of 661 pairwise comparisons in between-species category.

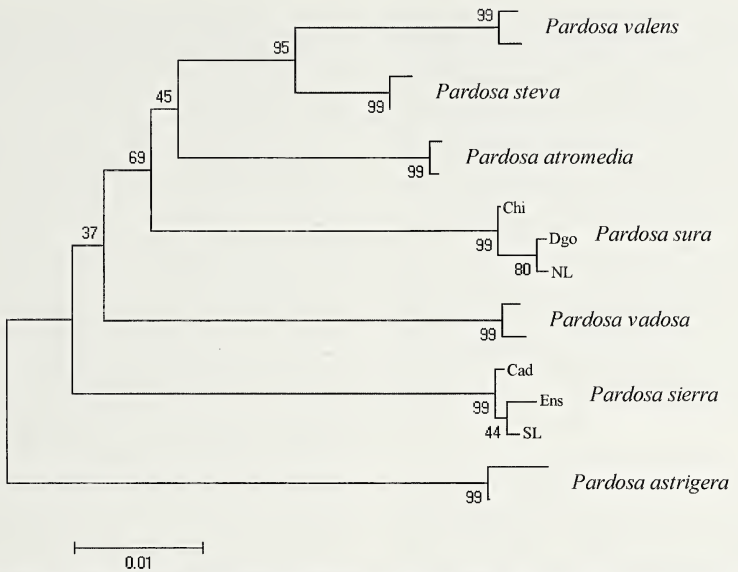

Figure 9.—Topology of neighbor-joining tree (Kimura-2 parameters; 10000 replicates of bootstrap) of COI mtDNA to some species of *lapidicina* group. The number in nodes indicates the statistical support of branches. Chi, Chihuahua; Dgo., Durango; NL, Nuevo León; Cad, Cadejé; SL, Sierra de la Laguna; Ens, Ensenada.

The nucleotide proportions of variable sites indicate that this region (COI) is a good indicator, not just for taxonomic information, but also for phylogenetic information because these species (*lapidicina* group) in this region are not saturated with transversions as in other species of invertebrates (de Oliveira et al. 2005; Yassin 2009). Hence, most changes are silent mutations, and just one change detected in an amino acid sequence corresponds to a transversion (A/G) in the base number 497 at the second position of the codon AAG (K/S) in two species *P. steva* and *P. atromedia*, data not shown. It will be necessary to include other species to corroborate this difference (Roe & Sperling 2007) and make a phylogenetic study of the *lapidicina* group.

The Gap Analysis was positive (+0.4), because it indicates the categories are isolated from each other. In other words they do not overlap between intraspecific and interspecific *p*-distance (Tables 4, 5) because the minimum variation between species is bigger than the maximum variation within species.

Based on morph differentiation, the minimal interspecific *p*-distance value of 2.46% divergence was found between the two morphologically differentiated species, as well as between *P. steva* and *P. valens*. We then confirmed the separation of *P. sierra* into three different species (Fig. 8) by using the value as a "threshold" of COI sequence divergence (Hebert et al. 2003, 2004; Barrett & Heber 2005; Astrin et al. 2006).

The three species' genetic distances of ~ 5–7% differentiation at the interspecific level indicate that these are genetically differentiated species, so the COI fragment that we selected is a good estimator for identification of species (Hebert et al. 2003, 2004; Paquin & Hedin 2004; Barrett & Hebert 2005; Astrin et al. 2006). Such results principally occur when these species are closely related, e.g., in the same species group, sibling or cryptic species as in other animals (arthropods: Hajibabaei et al. 2006; mammals: Clare et al. 2007; birds: Kerr et al. 2007). The levels of divergence found (Tables 4, 5) suggest that barcodes from COI can be used to distinguish among *Pardosa* species.

Additionally, the NJ tree shows that these species represent different groups, positioning *P. sierra* at the base, close to *P. vadosa* and *P. sura*; but *P. atromedia* is close to *P. valens* and *P. steva*. Finally, the branches indicate that lineage sorting is probably incomplete, although these lineages are separated enough to be considered as different reproductive units, forming a complex of cryptic species (Fig. 9).

Consequently, the use of DNA characteristics in a diagnostic context is entirely compatible with our taxonomic research. In this respect, we agree with Costa et al. (2007) that DNA barcoding is not a substitute for traditional taxonomy, but a good tool that has applications to delineate cryptic and sibling species and to resolve ecological questions. For example, many organisms that disperse by ballooning are immature, and it is almost always impossible to identify them to the species level (Greenstone et al. 1987; Greenstone 2001).

Regarding the distribution of species, *P. sierra* is restricted to Baja California Peninsula, *P. atromedia* is found in southern and central parts of California, and *P. sura* is the most widely distributed species, ranging from Oregon, northeastern parts of California, and Utah, USA to Veracruz

and Oaxaca, Mexico. We do not exclude the possibility that *P. sura* could be composed of sibling species, principally by its wide distribution range. Such species, if present, probably are hard to separate with somatic and genital morphology, but they could be differentiated with the use of the molecular markers employed herein. The lack of any specimen, either reported or collected, of *P. sura* in Sonora is probably the result of competitive exclusion and/or segregation in time between this species and *P. vadosa*, which was the dominant species in our samples taken from the northern parts of Sinaloa and the major parts of Sonora (> 400 specimens were recollected and checked from 13 sampled points).

In conclusion, our use of molecular data helped to delimit species that are difficult to diagnose based on morphological characters. More information, such as mate selection and hybridization between species could confirm these results, which would help to establish reliable species delineation. We think that the use of different data sets to test the concordance between species boundaries will be necessary in spider systematics in the future.

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New and poorly known species of the *mexicanus* group of the genus *Vaejovis* (Scorpiones: Vaejovidae) from Oaxaca, Mexico

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Abstract. Four new species belonging to the *mexicanus* group of the genus *Vaejovis* C.L. Koch 1836 from Oaxaca, Mexico are described. The number of species of this group for the state is raised to seven. The males of *V. franckei* and *V. setosus* are described for the first time. A key to Oaxacan species of the *mexicanus* group is provided.

Keywords: Scorpion, taxonomy, biodiversity, new species

The *mexicanus* group of the genus *Vaejovis* C.L. Koch 1836 has been one of the most neglected groups within this genus; it is also one of the rarest in collections (Sissom 2000). Originally recognized by Hoffmann (1931) as his "third section" of the genus, it was characterized by having the ventral submedian and ventrolateral carinae of metasomal segments I (or II) through IV well-developed and granular, and it included two species (one with three subspecies). Soleglad (1973) characterized this group based, among other characters, on the females having the genital opercula separated on the posterior fifth, and the basal position of chela trichobothria *ib-it*; he assigned eight species to it (three of which have since been transferred to the genus *Pseudouroctonus* Stahnke 1974). Sissom (1989) added six new species, and referred two others to the group. The same author (Sissom 2000) listed all the species assigned to that group up to 1998. Subsequently, Hendrixson and Sissom (2001) described two more taxa. The last three contributions cited mentioned that this group seems to be a widely distributed, heterogeneous assemblage of species that share the following characters: (1) six rows of denticles on the chela fixed finger, (2) the basal position of the *ib – it* trichobothria on the fixed finger, (3) stocky pedipalps, and (4) dark mottling on a brownish background color on most of the species. Since then the group received no attention until Graham (2007) described two species from the southwestern United States and placed them in this group. Soleglad & Fet (2008) assigned 28 species to the group, many of which do not belong here and will have to be re-assigned after a proper analysis (see Sissom 2000 for a preliminary discussion of the problem). Zárate-Gálvez & Francke (2009) recently described another new species from Chiapas. In addition to the characters mentioned above, and used by various authors to delimit the *mexicanus* group, we only consider as belonging to the group (= *mexicanus* group sensu stricto) those species in which (a) the spermatophore lacks a sclerotized mating plug, and (b) the telotarsus III distal spinule count is three (rarely) or higher (see McWest 2009). This restriction excludes *Vaejovis vorhiesi* Stahnke 1940 and its relatives (= group), found in mountains in the southwestern USA and northwestern Mexico, from the *mexicanus* group sensu stricto.

In recent years the number of species of scorpions from Oaxaca has increased from 25 reported by Lourenço & Sissom (2000) to 36 (Santibáñez-López et al., 2007), and Oaxaca is proving to be a region of high scorpion diversity (Francke 1977). The genus *Vaejovis* in Oaxaca is currently represented by eight species: three assigned to the *eusthenura* group, three to the *mexicanus* group and two to the *nitidulus* group. The present contribution is the description of four new species of the *mexicanus* group, two of them from the Northern Mountain Range (Sierra Madre Oriental) from Oaxaca, one from the Mixteca region and the other from the Southern Mountain Range (Sierra Madre Occidental). Therefore, the new diversity figures for Oaxaca are: 40 species, 12 *Vaejovis*, and seven belonging to the *mexicanus* group. Furthermore, the males of two previously known species are described for the first time.

METHODS

Nomenclature and mensuration primarily follow Stahnke (1970), except for trichobothrial terminology after Vachon (1974), metasomal carinal terminology after Francke (1977) and pedipalp carinal terminology after Acosta et al. (2008). Hemispermatophores were dissected follow Vachon (1952), and cleared using the technique of Alvarez & Hormiga (2007); terminology after Sissom (1991). Granular, used primarily to refer to carinae, indicates a linear, bead-like arrangement of granules; granulose, used for carinae and for surfaces, indicates a primarily random scattering of granules. Higher scorpion classification follows Prendini & Wheeler (2005). Measurements were taken using an ocular micrometer calibrated at 10X with a Nikon SMZ800 stereoscope and are given in millimeters. Drawings were obtained with a camera lucida supported on the same stereoscope. Photographs were taken with a Nikon Coolpix S10 VR camera attached to the same stereoscope. Drawings and photographs were edited with Adobe Photoshop © C3. Geographical coordinates were obtained in the field with a Garmin eTrex GPS; missing geographic data were obtained from the Localities Historical Archive of the INEGI, online at http://mapserver.inegi.org.mx/AHL/activaTiposBusqueda.do, and using Google Earth. Maps were made with ArcView © Version 3.2. Map base taken from CONABIO (Online at http://www.conabio.gob.mx/metacarto/metadatos.pl). Abbreviations for measurements (all given in mm): L = length; W = width; D = depth; $\bar{x}$ = average; ± = standard deviation. Abbreviations for depositories: AMNH – American Museum of Natural History, New York; CNAN – Colección Nacional de Arácnidos, Instituto de Biologia, Universidad Nacional Autónoma de México, México, D.F.; CALA – Colección Institucional "Luis de Armas" del Instituto Tecnológico del Valle de Oaxaca, Oaxaca, México.

Mesosomal sternite VII setal count.—Sissom (1989) was the first to mention the taxonomic relevance of this character; nevertheless he did not define a clear methodology to do it (e.g., the exclusion of marginal setae from the total count). Later, Hendrixson & Sissom (2001) reported the setae on the three species of their work, but they did not provide the methodology, either. Graham (2007) did not include this character in his descriptions. On many species of *Vaejovis*, stout, reddish macrosetae are associated with the submedian and lateral carinae, including the posterior margin of the sternite; but in the *mexicanus* group setae can also occur throughout the sternite. The only setae excluded from the counts reported in this paper are microsetae (= thin, colorless) and a few macrosetae that occur on the lateral margins of the sternite.

Metasomal setal count.—Setal counts in this region have been cited in previous descriptions, although variability has not been properly analyzed. A preliminary analysis based on 128 specimens belonging to 10 different taxa indicates to us that these meristic characters are of limited taxonomic value in the *mexicanus* group (Francke & Santibañez-Lopez, unpublished data) and are thus excluded from the specific diagnoses.

Telotarsus III distal spinule count.—Recently, McWest (2009) reported on the taxonomic usefulness of this character in vaejovid scorpions, based on a sample of numerous taxa, many of which where represented by one or few specimens. As pointed out by McWest (2009), telotarsus III seems to show the lowest variation. Hence we only considered the spinule count on that telotarsus. We consider it very important in the delimitation of the *mexicanus* group, and provide comprehensive counts for the seven species treated, to document the extent of intraspecific variation in this character.

KEY FOR THE IDENTIFICATION OF ADULTS OF OAXACAN SPECIES OF THE *MEXICANUS* GROUP

1. Species with metasomal segment III wider than long. Sternites with strong, contrasting dusky pattern. Adults < 22 mm long 2
   Species with metasomal segment III longer than wide. Sternites without dusky markings, or if present, weak to faint. Adults > 22 mm long 4
2. Metasomal segment V L/W ratio 1.42–1.93 3
   Metasomal segment V L/W ratio 3.00 ..... *V. dzahui* sp. nov.
3. Chela with eight granulose carinae (males unknown, data only from holotype female) ..... *V. nigrofemoratus* Hendrixson & Sissom 2001
   Chela with two carinae only, weakly granulose. ..... *V. franckei* Sissom 1989
4. Vesicle wider than posterior margin of metasomal segment V. Pedipalp chela fingers dentate margin on males with pronounced scalloping ..... *V. zapoteca* sp. nov.
   Vesicle as wide as the posterior margin of metasomal segment V. Pedipalp chela fingers dentate margin on males straight, without scalloping 5
5. Sternite VII with 11–12 setae. Chela with dorsal carinae moderate to strong, granulose ..... *V. darwini* sp. nov.
   Sternite VII with > 15 setae. Chela with dorsal carinae weak, granulose. 6
6. Pectinal tooth count on males = 18–20, on females = 17–18 ..... *V. prendinii* sp. nov.
   Pectinal tooth count on males = 15–16, on females = 13–15 ..... *V. setosus* Sissom 1989

SYSTEMATICS

Family Vaejovidae Thorell 1876
Genus *Vaejovis* C.L. Koch 1836

Vaejovis C.L. Koch 1836:51.

Type species.—*Vaejovis mexicanus* C.L. Koch 1836 by monotypy.

Vaejovis setosus Sissom 1989
(Figs. 2–8)

Vaejovis setosus Sissom 1989:152–154, 157, figs. 62–64, 66–71; Kovařík 1998:148; Sissom 2000:543; Soleglad & Fet 2008:100.

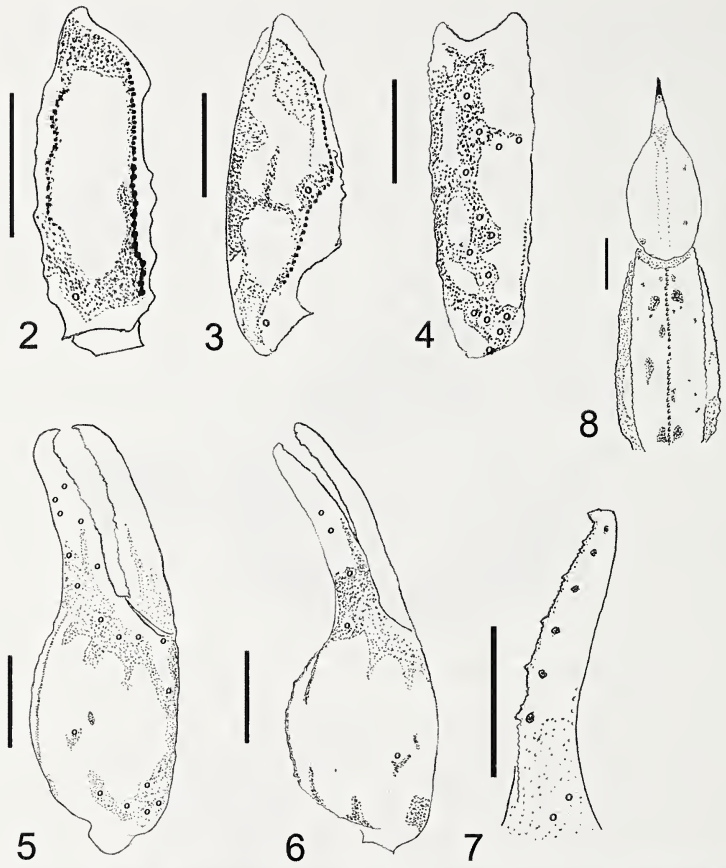
Type data.—MEXICO: *Oaxaca*: holotype female, Distrito Tlacolula, 3 mi SE of Tlacolula (16°56.000′N, 96°25.000′W), 30 August 1966, J. and W. Ivie (AMNH, not examined); 1 paratype female, Tlacolula, 16 June 1955, C. and P. Vaurie (AMNH, examined).

Material examined.—MEXICO: *Oaxaca*: 2♂, 3♀, 4 subadult ♂ and 2 juvenile ♀, Distrito Ixtlan de Juarez, km 45.8 federal road 175, Oaxaca-Ixtlan de Juarez (17°17.834′N, 96°32.582′W, elev. , masl), 14 June 2007, A. Valdez and C. Santibáñez (CNAN); 1♂, 1♀, same data (AMNH); 1♂, 1♀, 2 km road to San Juan Chicomezuchitl, (17°17.697′N, 96°29.980′W, elev. 1,584 masl), 15 June 2007, A. Valdez and C. Santibáñez (CNAN); 4♀, Km 171 road Ixtlan de Juarez-Oaxaca (17°17.835′N, 96°32.577′W, elev. 2,006 masl), 16 March 2008, A. Valdez, H. Montaño and C. Santibáñez (CNAN); 2♀, Distrito Mixes, Santa Maria Tlahuitoltepec, (17°01.037′N, 96°01.915′W, elev. 2,459 masl), 20 July 2007, O. Francke, A. Ballesteros, H. Montaño, C. Santibáñez and A. Valdez (CNAN); 1 ♀, Distrito Tlacolula, Yagul 30 km, 13 August 1988, S. Stockwell (AMNH).

Diagnosis.—Adults 17–28 mm long. Base color yellow brown with strong blackish markings on tergites, metasoma and appendages; chelicerae with dusky markings limited to distal margin. Pectinal tooth count on males 15–16 (mode = 15), on females 13–15 (mode = 14). Sternite VII with 16–21 setae (mode = 20). Segment V length/width mean = 1.85 (± 0.09) in females and mean = 2.07 (± 0.20) in males. Vesicle width/segment V posterior width mean = 1.23 (± 0.12) in females and mean = 1.25 (± 0.08) in males. Pedipalps: dorsal surfaces of femur and tibia finely granulose; patella with retrodorsal carina weak, smooth. Dentate margin of pedipalp fingers straight on both sexes. Dentate margin of movable finger with six subrows of denticles, with seven inner denticles. Telotarsus III with one ventromedial row of spinules bifurcating distally with 4–6 (mode = 2 pairs) spinules.

Appears most similar to *V. darwini* sp. nov. and *V. prendinii* sp. nov., which share a relatively large size (adults > 22 mm

Figure 1.—Distribution of the species of the "*mexicanus*" group of the genus *Vaejovis* Koch 1836 in Oaxaca, Mexico. *V. setosus* (✱); *V. franckei* (▲); *V. prendinii* (●); *V. zapoteca* (✚); *V. dzahui* (■); and *V. darwini* (●). The outline represents the Northern Mountain Range of Oaxaca. Elevation ranges in meters.



Figures 2–8.—*Vaejovis setosus* Sissom, male (from km 45.8 federal road 175, Oaxaca-Ixtlan de Juarez): 2. Right femur, dorsal view; 3. Right patella, dorsal view; 4. Right patella, retrolateral view; 5. Right chela, retrodorsal view; 6. Right chela, dorsal view; 7. Fixed finger, ventral view; 8. Metasomal segment V, ventral view. Scale bars = 1 mm.

long), metasomal segment III is longer than wide, and the lack of infuscations on the sternites. *V. darwini* sp. nov. has fewer setae on sternite VII (11–12) and a higher pectinal tooth counts (males 17, females 15–16); and *V. prendinii* sp. nov. also has a higher pectinal tooth count (males 18–20, females 17–18).

Description of male.—*Coloration:* Base color yellow brown with moderately strong dusky pattern (as female, see Sissom 1989).

Prosoma: Anterior margin of carapace weakly concave; surface sparsely granulose.

Mesosoma: Tergites sparsely, coarsely granular; shagreened. Tergites I–IV: median carina on I obsolete, on II–VI weak, granulose. Submedian carinae on I–II vestigial; on III–V weak, granulose; on VI moderate, granular. Tergite VII: median carina present on anterior two-thirds; submedian and lateral carinae strong, granular. Genital papillae well developed. Pectinal tooth count 15–15. Sternites III–VI smooth to shagreened medially; weakly to moderately setose. Sternite VII with one pair of weak, granular lateral carinae. Sternite VII with 16 setae.

Metasoma: Segments I–IV. Carination: Dorsolateral carinae on I strong, serrate to crenulate; on II–IV strong, crenulate. Lateral supramedian carinae on I–III strong, crenulate; on IV strong, crenulate to granular. Lateral inframedian carinae on I strong, granular; on II present only on posterior two-thirds, strong, granular to crenulate; on III present only on posterior half, strong to moderate, crenulate; on IV absent. Ventrolateral carinae on I moderate, irregularly crenulate; on II–IV strong, irregularly crenulate. Ventral

Table 1.—Variation in the pectinal tooth count in the eight species of the *Vaejovis* "*mexicanus*" group.

Species	Sex	10	11	12	13	14	15	16	17	18	19	20
V. setosus	male						12	2				
	female				8	9	1					
V. franckei	male			3	12	3						
	female	2	5									
V. prendinii sp. nov.	male									1	3	4
	female								2	2		
V. zapoteca sp. nov.	male			8	33	11	3					
	female		1	12	5	4						
V. dzahui sp. nov.	male				8	10	2					
	female			5	3							
V. darwini sp. nov.	male								6			
	female						1	3				
V. pusillus	male		2	2								
	female	2	4									
V. granulatus	male						1	3	4	2		
	female					4	5	1				

submedian carinae on I obsolete; on II weak, feebly granular; on III moderate, crenulate; on IV strong, irregularly crenulate. Intercarinal spaces shagreened. Segment V: Dorsolateral carinae strong, granular to serrate; lateral carinae moderate, granular to crenulate; ventrolateral carinae strong, granular to crenulate; ventromedian carina strong, granular to crenulate. Intercarinal spaces shagreened.

Telson: Vesicle wider than posterior margin of segment V (Fig. 8); ventral surface irregularly granular, with 4 pairs of setae; subtle subaculear tooth preceded by a few small granulations.

Pedipalps: Orthobothriotaxic "C". Femur (Fig. 2): Dorsal surface with some coarse granulation, shagreened. Prodorsal carina moderate, granular to crenulate. Retrodorsal carina moderate to weak, granular. Proventral carina strong, granular. Retroventral carina weak, smooth. Setation (right/left): prodorsal carinae with 5/6 setae, 5/5 medial setae on prolateral face; retroventral carinae with 3/4 setae. Patella (Figs. 3, 4) with retrodorsal carina weak, smooth; prodorsal carina moderate, granular to crenulate; retroventral carina obsolete to faint, smooth; proventral carina weak, granular. Setation (right/left): prolateral face with 5/4 (right/left) setae. Chela (Figs. 5, 6) slender; dentate margins of fingers straight. Dorsal marginal, prodorsal, dorsal secondary and prolateral carinae weak, smooth; all other carinae obsolete. Fixed finger (Fig. 7) with primary denticle row divided into six subrows by five enlarged primary row denticles; six inner denticles. Movable finger with primary row divided into six subrows by five enlarged primary row denticles; seven inner denticles.

Legs: Basitarsus I with two ventrosubmedian rows of spinules. Basitarsus II with one ventrosubmedian row of spinules divided by 3 large setae. Basitarsi III–IV with one ventrosubmedian row of spinules divided by 4 large setae. Telotarsus III with one ventromedian row of spinules bifurcating distally, with four spinules (2 pro- and 2 retrolateral) on each leg.

Hemispermatophore: (Figs. 44, 45). Lamelliform; hooks basal, short, bifurcate; lamella thick and curved; no sclerotized hemi-mating plug.

Measurements: Total L, 21.5; carapace L, 3.1; mesosoma L, 5.6; metasoma L, 10.5. Metasomal segments: I L/W, 1.5/1.9; II L/W, 1.6/1.9; III L/W, 1.8/1.9; IV L/W, 2/1.8; V L/W/D, 3.6/1.7/1.7. Telson: Vesicle L/W/D, 2.3/1.4/1.1. Pedipalp: Total L, 9.7; femur L, 2.3; patella L/W, 2.9/0.9; chela L/W/D, 4.5/1.4/1.6; fixed finger L, 2.1; movable finger L, 2.8.

Variation: Vaejovis setosus shows no marked sexual dimorphism except in genital and pectinal characters, as shown by other congeners. Pectinal tooth count variation in Table 1. Sternite VII setae count ($n = 20$) 16–21 (mode = 20). There was no variation in the pedipalp chela finger dentition, all specimens have six subrows of denticles on both fingers; on the fixed finger all specimens have six inner accessory denticles, whereas on the movable finger all have seven. Telotarsus III distal spinule count ($n = 24$) 1 telotarsus with 3 spinules (1 pro- and 2 retrolateral), 19 with 4 (2 + 2) spinules, 3 with 5 (2 + 3) spinules and 1 with 6 (3 + 3) spinules.

Morphometric ranges: Males ($n = 7$): Chela L/W, 3.13–4.13; patella L/W, 2.70–3.33; fixed finger L/chela L, 0.11–0.49; segment V L/W, 1.64–2.22; vesicle W/posterior margin of segment V, 1.14–1.56. Females ($n = 9$): Chela L/W, 3.50–4.08; patella L/W, 2.73–3.43; fixed finger L/chela L, 0.44–0.54; segment V L/W, 1.65–2.00; vesicle W/posterior margin of segment V, 1.09–1.40.

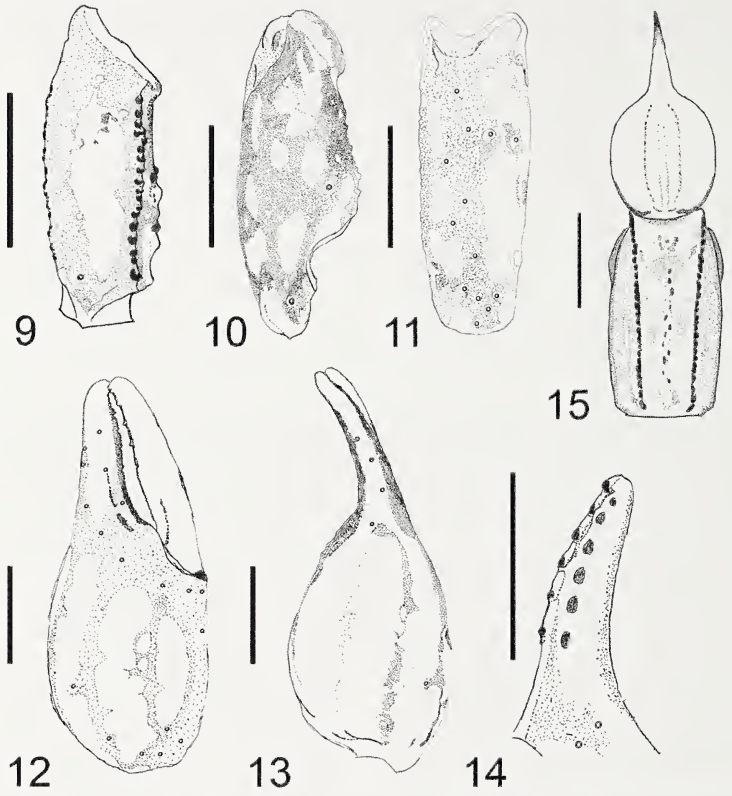
Distribution.—This species is known from the central mountains of Oaxaca and the Sierra Juarez (Ixtlan de Juarez district) (Fig. 1).

Vaejovis franckei Sissom 1989
(Figs. 9–15)

Vaejovis franckei Sissom 1989:150–152, 157, figs. 54–61; Kovařík, 1998:146; Sissom, 2000:540; Soleglad & Fet, 2008:99.

Type data.—MEXICO: *Oaxaca*: holotype female, Distrito Etla, Sierra Aloapaneca, 8–18 mi (via road) NNE of San Juan del Estado (17°16.446′N, 96°47.918′W, elev. 8,400–9,700 ft), 5 August 1966, C.M. and M.R. Bogert (AMNH, examined); 2 paratype females, Distrito Ixtlan de Juarez, El Punto, N of Continental Divide on road to Guelatao (17°13.025′N, 96°35.096′W, elev. 7,000–7,500 ft), 28 June 1967, M.R. Bogert (AMNH, not examined).

Other material examined.—MEXICO: *Oaxaca*: 4♂, 4♀, Distrito Ixtlan de Juarez, 6 km W Llano Grande, San Antonio



Figures 9–15.—*Vaejovis franckei* Sissom, male (from 6 km W of Llano Grande, San Antonio Cuajimolas): 9. Right femur, dorsal view; 10. Right patella, dorsal view; 11. Right patella, retrolateral view; 12. Right chela, retrodorsal view; 13. Right chela, dorsal view; 14. Fixed finger, ventral view; 15. Metasomal segment V, ventral view. Scale bars = 1 mm.

Cuajimoloyas (17°08.109′N, 96°26.576′W, elev. 3,134 masl), 20 June 2007, A. Valdez and C. Santibáñez, (CNAN); 2♂, 1♀, same data (AMNH); 5♂, 1♀, Distrito Etla, 10 km E San Pablo Etla (17°10.01′N, 96°41.11′W, no elevation), 3 March 2006, C. Santibáñez (CNAN); 1♂, La Carbonera, Telixtlahuaca (17°17.043′N, 96°56.238′W, no elev.), no collector (AMNH).

Diagnosis.—Adults 19–26 mm long. Base color yellow brown with strong blackish markings on tergites, sternites, metasoma and appendages; chelicerae with dusky markings limited to distal margin. Pectinal tooth count on males 12–14 (mode = 13), on females 10–11 (mode = 11). Sternite VII with 10–12 setae (mode = 10). Metasomal segments short and wide, vesicle width/segment V posterior width mean = 1.36 (± 0.18) in females and mean = 1.30 (± 0.16) in males. Lateral faces of metasomal segment V strongly convex. Pedipalps: retrodorsal carina of patella obsolete; retroventral carina obsolete or weak, smooth; sexual dimorphism present, with chela on males rounder than on females; dentate margin of movable finger divided into six subrows, with seven inner denticles. Telotarsus I–V with one ventromedian row of spinules bifurcating distally, with 4–6 (mode = 4) spinules.

Vaejovis franckei may be distinguished from *V. setosus* by the following characters: (1) metasomal segment V length/width ranges from 1.42–1.59 (not 1.76–1.86); (2) metasomal segment I dorsolateral carinae and lateral supramedian carinae are flanked in *V. setosus* by one seta (*V. franckei* is flanked by none); (3) sternite VII possesses 10–12 setae (16–20 in *V. setosus*); (4) cuticular surfaces, especially the carapace, metasoma, and pedipalps, are densely and coarsely granulose (at most, sparsely coarsely granulose in *V. setosus*); (5) pectinal tooth counts of 13–15 on females of *V. setosus* (not 10–11 as in *V. franckei*); (6) smaller body size; (7) on males the pedipalp chela is rounded with fingers shorter than the manus, whereas on *V. setosus* the chela is slender and it has fingers longer than the manus.

Description of male.—*Coloration:* Base color yellow brown; fuscous markings on tergites, metasoma and appendages strong; ventrally base color light yellow to light brown; sternites and pectines heavily mottled. Chelicerae with dusky markings limited to distal margins; most of cheliceral dorsal surface creamy yellow.

Prosoma: Anterior margin of carapace straight to weakly emarginated; surface around median eyes densely, finely granular interspersed with scattered coarse granules.

Mesosoma: Tergites sparsely, coarsely granulose; shagreened. Tergites I–VI: median carina on I obsolete, on II–VI weak, feebly granulose. Submedian carinae on I–II vestigial; on III–V weak, granular; on VI moderate, granular. Tergite VII: median carina present on anterior two-thirds; submedian and lateral carinae strong, granulose. Genital papillae well developed. Sternites III–VI smooth to shagreened medially, with dusky markings; sparsely setose. Sternite VII with one pair weak, feebly granulose lateral carinae. Sternite VII with 10 setae. Pectinal tooth count 13–13.

Metasoma: Segments I–IV: intercarinal spaces densely, coarsely granulose. Dorsolateral carinae on I strong, granular to crenulate; on II–IV strong, crenulate. Lateral supramedian carinae on I–III strong, crenulate; on IV strong, crenulate to granular. Lateral inframedian carinae on I strong, granular; on II present only on posterior half, strong, granular to serrate; on III present only on distal one-third, strong, serrate; on IV absent. Ventrolateral carinae on I moderate, irregularly crenulate; on II–IV strong, irregularly crenulate. Ventral submedian carinae on I obsolete; on II weak, granular; on III moderate, granular to crenulate; on IV strong, irregularly crenulate. Segment V: Dorsolateral carinae moderate, granular to crenulate; lateral carinae weak to moderate, granular; ventrolateral carinae strong, granular to crenulate; ventromedian carina moderate to strong, granular to crenulate. Intercarinal spaces densely, coarsely granular.

Telson: Vesicle 1.33 wider than the posterior margin of segment V; ventral surface irregularly granulose, with 4 pairs of setae (Fig. 15).

Pedipalps: Orthobothriotaxic "C". Femur (Fig. 9): Dorsal surface densely, finely granulose with some coarse granulation. Prodorsal carina strong, granular to crenulate. Retrodorsal carina moderate to weak, granular. Proventral carina weak, granular. Retroventral carina weak, smooth. Setation (right/left): prodorsal carinae with 4/4, 2/2 medial setae on prolateral face; retroventral carinae with 3/3. Patella (Figs. 10, 11) with retrodorsal carina obsolete; prodorsal carina moderate, crenulate to smooth; retroventral carina obsolete to faint, smooth; proventral carina weak, granular. Setation (right/left): 4/4 prodorsal setae. Chela (Figs. 12, 13) rounded, short. Digital, prodorsal, dorsal secondary and prolateral carinae weak, smooth; all other carinae obsolete. Fixed finger (Fig. 15) with primary row divided into six subrows by five enlarged primary row denticles; six inner denticles. Movable finger with primary row divided into six subrows by five enlarged primary row denticles; seven inner denticles.

Legs: Basitarsus I with two ventrosubmedian rows of spinules. Basitarsus II with one ventrosubmedian row of spinules divided by 3 large setae. Basitarsus III–IV with one ventrosubmedian row of spinules divided by 4 large setae. Telotarsus III with one ventromedial row of spinules bifurcating distally with four spinules (2 pro- and 2 retrolateral) on each leg.

Hemispermatophore: Lamelliform; hooks basal, short; lamella thick and curved; no sclerotized hemi-mating plug (Figs. 46, 47).

Measurements: Total L, 19.5; carapace L, 2.6; mesosoma L, 6.5; metasoma L, 8.4. Metasomal segments: I L/W, 1/1.8; II L/W, 1.3/1.7; III L/W, 1.4/1.7; IV L/W, 1.8/1.7; V L/W/D, 2.9/1.8/1.4. Telson: Vesicle L/W/D, 2/1.6/1.1. Pedipalp: Total L, 8.6; femur L, 2; patella L/W, 2.4/0.9; chela L/W/D, 4.2/1.4/1.7; fixed finger L, 1.6; movable finger L, 2.4.

Variation.—*Vaejovis franckei* shows marked sexual dimorphism on pedipalps: males with chela rounded, whereas on females they are slender. Pectinal tooth count variation in Table 1. Sternite VII setae count (n = 20) 10–12 (mode = 12). Pedipalp chela finger dentition (n = 20) for the right fixed finger, 18 fingers have 6 subrows of denticles and 2 have 5 subrows; 20 fingers have 6 inner accessory denticles. For the right movable finger, 20 fingers have 6 subrows of denticles; 20 fingers have 7 inner accessory denticles. Telotarsus III distal spinule count (n = 28): 24 with 4 (2 + 2), 3 with 5 (2 + 3) and 1 with 6 (3 + 3) spinules.

Morphometric ranges: Males (n = 9): Chela L/W, 2.56–3.00; patella L/W, 2.22–3.14; fixed finger L/chela L, 0.35–0.44; segment V L/W, 1.42–1.93; vesicle W/posterior margin of segment V, 1.08–1.55. Females (n = 4): Chela L/W, 3.60–3.90; patella L/W, 2.44–2.67; fixed finger L/chela L, 0.44–0.47; segment V L/W, 1.44–1.59; vesicle W/posterior margin of segment V, 1.17–1.55.

Distribution.—This species is known from the central mountains from Oaxaca and the Sierra Juarez (Distritos Ixtlan de Juarez and Etla) (Fig. 1).

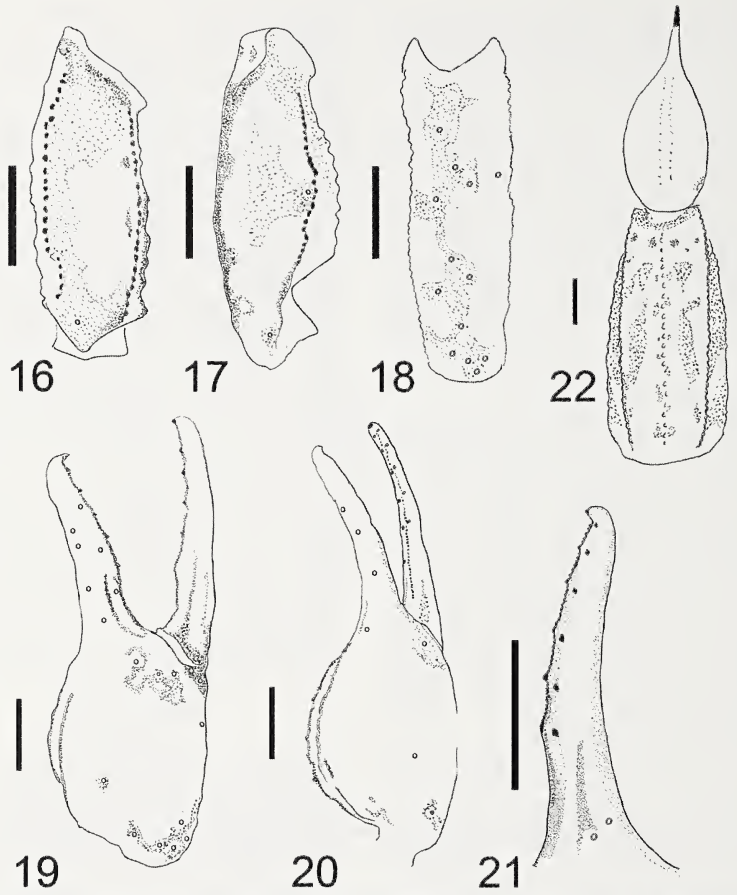
Vaejovis prendinii sp. nov.
(Figs. 16–22)

Type data.—MEXICO: *Oaxaca*: holotype male, Distrito Ixtlan de Juarez, Rio Grande, San Juan Atepec (17°24.837′N, 96°34.265′W, elev. 1,327 masl), 3 July 2008, O. Francke, A. Quijano and C. Santibáñez (CNAN-T0378). Paratypes: 1 male, 1 female, collected with holotype (CNAN-T0379); 1 female, collected with holotype (AMNH); 1 male, 2 km NW of San Juan Atepec (17°25.774′N, 96°33.314′W, elev. 1,849 masl), 4 July 2008, O. Francke, A. Quijano and C. Santibáñez (CNAN-T0380).

Other material examined.—MEXICO: *Oaxaca*: 1♂, Distrito Ixtlan de Juarez, Ixtlan de Juarez (17°19.596′N, 96°28.891′W, no elev.), no date, no collector (CNAN-S00628); 1 juvenile, Ixtlan de Juarez (17°19.596′N, 96°28.891′W, no elev.), 24 April 2004, G. Linares (CALA).

Etymology.—The specific epithet is a patronym honoring Dr. Lorenzo Prendini (AMNH) for his contributions to scorpion systematics.

Diagnosis.—Adults 25–34 mm long. Sexual dimorphism present; males with weak scalloping in the fingers on the pedipalp chela. Sternite VII with 20–23 setae (mode = 22). Pectinal tooth count: males 18–20 (mode = 20), and females 17–18 (mode = 17–18). Vesicle width/segment V posterior margin mean = 1.19 (± 0.15) in males. Dentate margin of movable finger of pedipalp chela with six subrows of denticles, seven inner denticles.



Figures 16–22.—*Vaejovis prendinii* sp. nov., holotype male: 16. Right femur, dorsal view; 17. Right patella, dorsal view; 18. Right patella, retrolateral view; 19. Right chela, retrodorsal view; 20. Right chela, dorsal view; 21. Fixed finger, ventral view; 22. Metasomal segment V, ventral view. Scale bars = 1 mm.

Vaejovis prendinii is most similar to *V. franckei*, from which it can be distinguished by: (1) metasomal segments proportionately shorter in *V. franckei*; (2) sternite VII with 20–23 setae (10 setae on *V. franckei.*); (3) metasomal carinae more hirsute than in *V. franckei*; (4) pectinal tooth count on males considerably higher (18–20; mode = 20) whereas on *V. franckei* it is lower (12–14); on females also significantly higher 17–18, whereas on *V. franckei* 10–11.

Vaejovis prendinii can be distinguished from *V. setosus* by: (1) pectinal tooth count in males = 18–20 (mode = 20) on *V. prendinii*, whereas in *V. setosus* on males = 15–16 (mode = 15); (2) adults bigger than *V. setosus*; (3) sternite VII with 20–23 setae (mode = 22), whereas *V. setosus* has 16–21 setae (mode = 20); (4) males with chela globose, whereas on *V. setosus* it is slender (see Figs. 5, 6, 19, 20).

Vaejovis prendinii is also similar to *V. granulatus* but it is distinguished by: (1) pectinal tooth count on males = 18–20 (mode = 20), whereas on *V. granulatus* it is 15–19 (mode = 18); (2) metasomal dorsolateral carinae on segment I flanked by three setae, whereas on *V. granulatus* it is flanked by two; (3) pedipalp chela movable finger dentition divided into 6 subrows with 7 inner accessory granules (5 subrows with 6 inner accessory granules on *V. granulatus*); (4) Sternite VII with 20–23 setae (10 setae on *V. granulatus*).

Description of holotype male.—*Coloration:* Body base color yellow brown with moderately strong dusky pattern, pedipalp chela light orange with the finger tips brown.

Prosoma: Anterior margin of carapace weakly concave, entire surface shagreened, sparsely granulose.

Mesosoma: Tergites shagreened. Tergites I–VI: median carina on I–II obsolete, on III–VI weak, granulose. Submedian carinae on I–II vestigial, on III–IV weak, granulose, on V–VI moderate, granular. Tergite VII: median carina present on anterior two-thirds, submedian and lateral carinae strong, granular. Genital papillae developed. Pectinal tooth count 19–19. Sternites III–VI smooth to shagreened medially, moderately to densely setose. Sternite VII with submedian carinae weak, smooth to feebly crenulate; lateral carinae weak, granular. Sternite VII with 22 setae.

Metasoma: Segments I–IV: dorsolateral carinae on I–II strong, granular; on III–IV strong, granular to crenulate. Lateral supramedian carinae on I–III strong, crenulate to serrate; on IV moderate, crenulate to granular. Lateral supramedian carinae on I–III strong, crenulate; on IV moderate, crenulate to granular. Lateral inframedian carinae on I strong, granular; on II present only on posterior half, moderate, granular to crenulate; on III present only on posterior one-third, moderate, crenulate; on IV absent. Ventrolateral carinae on I strong, granular to crenulate; on II–IV strong, irregularly crenulate. Ventral submedian carinae on I weak, smooth to crenulate; on II–III moderate, granular to crenulate; on IV strong, crenulate. Intercarinal spaces shagreened. Segment V: dorsolateral carinae moderate, crenulate to serrate; lateral carinae weak, present only on anterior half, crenulate; ventrolateral carinae strong, crenulate; ventromedian carina moderate, granular; intercarinal spaces shagreened.

Telson: Vesicle as wide as posterior margin of segment V; ventral surface with 12 setae (Fig. 22).

Pedipalps: Orthobothriotaxic "C". Femur (Fig. 16): Dorsal surface with few coarse granulations, shagreened. Prodorsal carina strong, granular. Retrodorsal carina moderate to weak, crenulate. Proventral carina moderate, granular. Retroventral carina weak to moderate, feebly granular. Setation (right/left): prodorsal carinae with 3/3 setae, 3/3 medial setae on prolateral face; retroventral carinae with 4/4 setae. Patella (Figs. 17, 18) with retrodorsal carina weak, smooth; prodorsal carina moderate, granular to crenulate; retroventral carina obsolete to faint, smooth; proventral carina moderate, granular. Setation (right/left): 5/6 setae on prolateral face. Chela (Figs. 19, 20) with weak scalloping on the fingers. Digital, prodorsal, dorsal secondary and retrolateral carinae weak, crenulate to smooth; two prolateral carinae present (dorsal and ventral), dorsal weak to moderate, granular; ventral weak, smooth to feebly crenulate; all other carinae obsolete. Fixed finger (Fig. 21) with primary row divided into six subrows by five enlarged primary row denticles; six inner denticles. Movable finger with primary row divided into six subrows by five enlarged primary row denticles; distal-most row very short with a single denticle; seven inner denticles.

Legs: Basitarsus I–III with two ventrosubmedian rows of spinules, divided by four large setae. Basitarsus IV with two ventrosubmedian rows of four setae. Telotarsus III with ventromedial row of spinules bifurcating distally, with five spinules (2 pro- and 3 retrolateral) on one leg, and four spinules (2 pro- and 2 retrolateral) on the other leg.

Hemispermatophore: Lamelliform; hooks basal, short; lamella straight and wide; no sclerotized hemi-mating plug (Figs. 48, 49).

Measurements: Holotype male: Total L, 30.4; carapace L, 3.7; mesosoma L, 9.2; metasoma L, 14.6. Metasomal segments: I L/W, 1.9/2.4; II L/W, 2.2/2.2; III L/W, 2.4/2.2; IV L/W, 3.2/2.2; V L/W/D, 4.9/2.3/2. Telson: Vesicle L/W/D, 2.9/1.8/1.3. Pedipalp: Total L, 13.2; femur L, 3.3; patella L/W, 3.6/1.1; chela L/W/D, 6.3/1.8/2.1; fixed finger L, 2.4; movable finger L, 3.6.

Paratype female: Total L, 32.5; carapace L, 4.3; mesosoma L, 11.6; metasoma L, 13.8. Metasomal segments: I L/W, 1.8/2.6; II L/W, 2.1/2.5; III L/W, 2.3/2.5; IV L/W, 3.2/2.4; V L/W/D, 4.4/2.3/2.1. Telson: Vesicle L/W/D, 2.8/1.9/1.6. Pedipalp: Total L, 13.8; femur L, 3.4; patella L/W, 3.8/1.1; chela L/W/D, 6.6/1.7/1.9; fixed finger L, 2; movable finger L, 4.1.

Variation.—*Vaejovis prendinii* exhibits some sexual dimorphism: males with weak scalloping present in the fixed fingers; males with proportionately longer metasomal segments than females. Pectinal tooth count variation in Table 1. Sternite VII setae count (n = 5) 20 to 23 (mode = 22). On the pedipalp chela fixed finger all specimens have six subrows and six inner accessory denticles; on the movable finger all specimens have six subrows (distal most always very short with only one or two denticles) and seven inner accessory denticles. Telotarsus III distal spinule count (n = 5): 7 with 4 (2 + 2) and 3 with 5 (2 + 3) spinules.

Morphometric ranges: Males (n = 4): Chela L/W, 2.95–3.50; patella L/W, 3.09–3.33; fixed finger L/chela L, 0.38–0.41; segment V L/W, 2.00–2.20; vesicle W/posterior margin of segment V, 1.00–1.33. Females (n= 2): Chela L/W, 3.53–3.88; patella L/W, 3.45–3.55; fixed finger L/chela L, 0.30–0.50; segment V L/W, 1.91–2.04; vesicle W/posterior margin of segment V, 1.19–1.20.

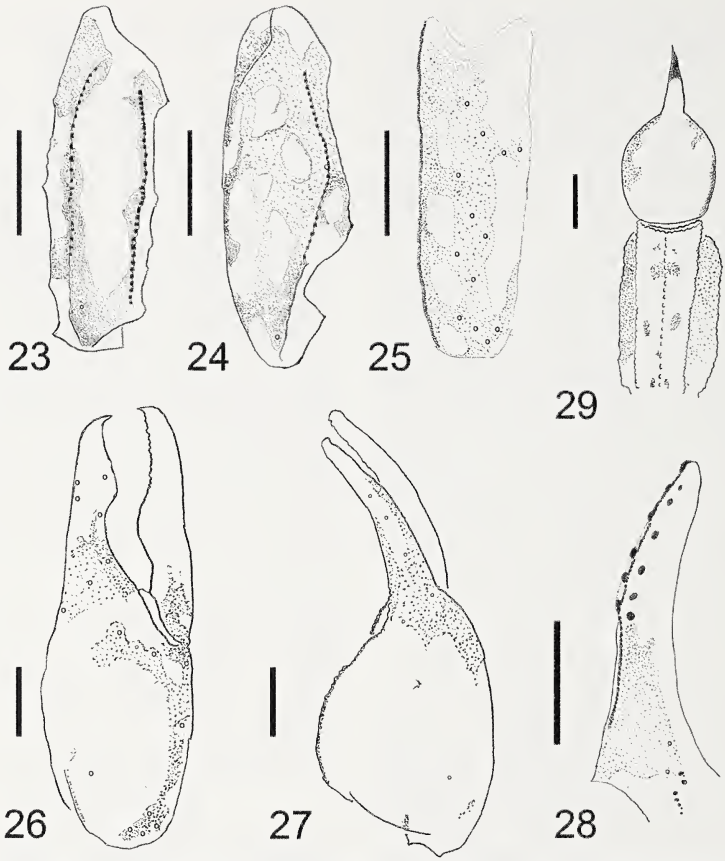
Distribution.—This species is known from the type locality, and one additional locality nearby, in Ixtlan district (Fig. 1).

Vaejovis zapoteca sp. nov.
(Figs. 23–29)

Vaejovis franckei: Mondragon & Cruz-Ruiz, 2009:371 (misidentification).

Type data.—MEXICO: *Oaxaca*: holotype male, Distrito Ixtlan de Juarez, Puerta del Sol, San Pablo Macuiltianguis (17°31.722′N, 96°33.678′W, elevation 2,742 masl), 13 November 2005, O. Francke, G. Montiel, M. Córdova, A. Jaimes and C. Santibáñez (CNAN-T0381). Paratypes: 5 males, 2 females, collected with holotype (CNAN-T0382); 5 males, 1 female, collected with holotype (AMNH).

Other material examined.—MEXICO: *Oaxaca*: 15♂, 3♀, Distrito Ixtlan de Juarez, Campamento Tatachinto, Santiago Xiacui (17°17.254′N, 96°25.058′W, elev. 2,313 masl), 22 July 2007, O. Francke, A. Ballesteros, H. Montaño, C. Santibáñez and A. Valdez (CNAN); 5 ♂, km 137 road Oaxaca-Tuxtepec (17°24.292′N, 96°30.595′W, elev. 2,789 masl), 23 July 2007, O. Francke, A. Ballesteros, H. Montaño, C. Santibañez and A. Valdez (CNAN); 2♂, 5♀, 1 km E Campamento del Monte, El Punto, Santa Catarina Ixtepeji (17°11.704′N, 96°35.898′W, elev. 2,537 masl), 17 March 2008, H. Montaño, C. Santibáñez and A. Valdez (CNAN).



Figures 23–29.—*Vaejovis zapoteca* sp. nov., holotype male: 23. Right femur, dorsal view; 24. Right patella, dorsal view; 25. Right patella, retrolateral view; 26. Right chela, retrodorsal view; 27. Right chela, dorsal view; 28. Fixed finger, ventral view; 29. Metasomal segment V, ventral view. Scale bars = 1 mm.

Etymology.—The specific epithet is derived from the name of the Zapoteca culture, which inhabits the area of distribution of this species; it is used as a noun in apposition.

Diagnosis.—Adults 28–30 mm long. Sexual dimorphism present on pedipalp chela, males with swollen pedipalp chelae and pronounced scalloping in the fingers. Sternite VII with 10–11 setae (mode = 10). Pectinal tooth count on males 12–15 (mode = 13), on females 11–14 (mode = 12). Vesicle width/segment V posterior margin mean = 1.58 (± 0.09) in males. Pedipalp chela movable finger with 6 subrows of denticles divided by 5 enlarged denticles, 7–10 (mode = 8) inner denticles.

Vaejovis zapoteca is similar to *V. franckei* but it differs as follows: (1) sternites with strong dusky markings, whereas on *V. zapoteca* with faint to obsolete dusky marking pattern; (2) vesicle width/posterior margin of metasomal segment V is mean = 1.30 (± 0.16) in males of *V. franckei*, whereas in *V. zapoteca* mean is = 1.58 (± 0.09); (3) pedipalp movable finger with 6 subrows in *V. franckei*, whereas on *V. zapoteca* there are 5 subrows; (4) pedipalp movable finger with 6 inner accessory denticles in *V. franckei*, whereas on *V. zapoteca* there are usually more than 6 (see intraspecific variation above).

Vaejovis zapoteca may be distinguished from *V. setosus* as follows: (1) males with scalloping pronounced on the pedipalp chela fingers, whereas on *V. setosus* it is absent; (2) pectinal tooth count on males = 12–15 (mode = 13), whereas on *V. setosus* 15–16 (mode = 15); (3) dorsolateral carinae on segment I with one seta (two setae on *V. setosus*); (4) sternite

VII with 10–11 setae (mode = 10) on *V. zapoteca* (16–21, mode = 20 on *V. setosus*); (5) vesicle width/posterior margin of metasomal segment V in *V. zapoteca* males mean = 1.58 (± 0.09), whereas in *V. setosus* mean = 1.25 (± 0.08); (6) movable finger on *V. setosus* with six inner accessory denticles, whereas on *V. zapoteca* there are usually 8–9 inner accessory denticles.

Vaejovis zapoteca is also similar to *V. prendinii* and it may be separated by the following characters: (1) males with pedipalp chela fingers with scalloping pronounced in *V. zapoteca*, whereas on *V. prendinii* they are weakly scalloped; (2) pectinal tooth count on males 12–15 (mode = 13) (18–20, mode = 20 on *V. prendinii*); (3) sternite VII with 20–23 (mode = 22) setae on *V. prendinii*, whereas on *V. zapoteca* with 10–11 (mode = 10); (4) vesicle width/posterior margin of metasomal segment V in males mean = 1.58 (± 0.09), whereas in *V. prendinii* mean = 1.19 (± 0.15); (5) pedipalp chela movable finger with 8–9 inner denticles (6 inner denticles on *V. prendinii*).

Finally, *Vaejovis zapoteca* may be distinguished from *V. granulatus* by: (1) pectinal tooth count on males = 12–15 (mode = 13), whereas on *V. granulatus* 15–18 (mode = 17); (2) metasomal dorsolateral carinae on segment I flanked by 1 seta (2 on *V. granulatus*); (3) chela length/width 2.62 on males (3.05 on males in *V. granulatus*).

Description of holotype male.—*Coloration:* Body base color orange brown with moderately strong dusky pattern, pedipalp chela light orange with the fingers brown.

Prosoma: Anterior margin of carapace weakly concave; entire surface shagreened, sparsely granulose.

Mesosoma: Tergites shagreened. Tergites I–VI: median carina on I–II obsolete, on III–VI weak, granulose; submedian carina on I vestigial, on II weak, granular present only on the post tergite, on III–VI moderate, granular present only on the post tergite. Tergite VII: median carina present on anterior two-thirds, submedian and lateral carinae strong, granular, present only on posterior half. Genital papillae developed. Pectinal tooth count 14–14. Sternites III–VI smooth to shagreened medially, sparsely setose. Sternite VII with submedian carinae weak, smooth; lateral carinae weak, granular. Sternite VII with 10 setae.

Metasoma: Dorsolateral carinae on I–II strong, granular to crenulate; on III–IV strong, crenulate. Lateral supramedian carinae on I–IV strong, crenulate. Lateral inframedian carinae on I strong, granular; on II present only on posterior one-third, moderate, granular to crenulate; on III present only on posterior one fifth, weak, granular; IV absent. Ventrolateral carinae on I–IV strong, irregularly crenulate. Ventral submedian carina on I moderate, smooth to crenulate; on II–IV strong, smooth to crenulate. Intercarinal spaces shagreened. Segment V: Dorsolateral carinae moderate, smooth to crenulate; lateral carinae moderate, present on anterior two-thirds, crenulate; ventrolateral carinae strong, crenulate to granular; ventromedian carina strong, granular; intercarinal spaces shagreened.

Telson: Vesicle 1.53 times wider than posterior margin of segment V (Fig. 29).

Pedipalps: Orthobothriotaxic "C". Femur (Fig. 23). Dorsal face with sparse, coarse granulation, shagreened. Prodorsal carina strong, granular. Retrodorsal carina moderate to weak, granular to crenulate. Proventral carina moderate, granular. Retroventral carina weak to faint, smooth. Setation (right/left): prodorsal carinae with 1/1 dorsal seta, 2/2 medial setae on prolateral face; retroventral carinae with 1/2 setae. Patella (Figs. 24, 25) with retrodorsal carina weak, smooth; prodorsal carina moderate, granular; ventroexternal carina obsolete to vestigial, smooth; ventrointernal carina weak, granular. Setation (right/left): 3/3 setae on prolateral face. Chela (Figs. 26, 27) rounded, scalloping strong on the fingers. Digital, prodorsal and dorsal secondary carinae weak to vestigial, smooth; two prolateral carinae (dorsal and ventral) weak, granulose; all other carinae obsolete. Fixed finger (Fig. 28) with primary row divided into six subrows by five enlarged primary row denticles; six inner accessory denticles; movable finger with primary row divided into six subrows by five enlarged primary row denticles, eight inner denticles.

Legs: Basitarsus I–II with two ventrosubmedian rows of spinules, divided by three large setae. Basitarsus III with one ventrosubmedian row of spinules divided by three large setae. Basitarsus IV consist of two rows of four large setae. Telotarsus III with ventromedial row of spinules bifurcating distally, with two pairs of spinules on each leg.

Hemispermatophore: (Figs. 50, 51). Lamelliform; hooks short, bifurcate, basal; lamella curved and wide; no sclerotized hemi-mating plug.

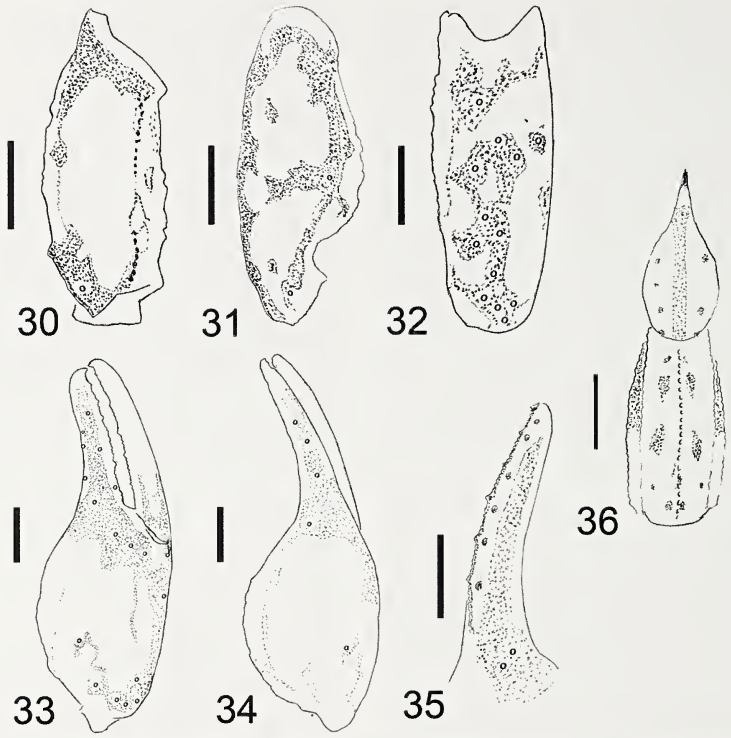
Measurements.—*Holotype male:* Total L, 31.1; carapace L, 3.8; mesosoma L, 11.5; metasoma L, 13.3. Metasomal segments: I L/W, 1.7/2.2; II L/W, 2.1/2.2; III L/W, 2.4/2.1; IV L/W, 3.1/2.1; V L/W/D, 4.0/2.0/2.0. Telson: Vesicle L/W/D, 2.5/2.3/1.4. Pedipalp: Total L, 13.1; femur L, 3.2; patella L/W, 3.6/1.1; chela L/W/D, 6.3/2.4/2.3; fixed finger L, 2.6; movable finger L, 3.6.

Paratype female: Total L, 27.1; carapace L, 3.6; mesosoma L, 9.8; metasoma L, 11.4. Metasomal segments: I L/W, 1.5/2.2; II L/W, 1.9/2.0; III L/W, 2.0/1.9; IV L/W, 2.5/1.8; V L/W/D, 3.5/1.8/1.7. Telson: Vesicle L/W/D, 2.3/1.7/1.1. Pedipalp: Total L, 11.4; femur L, 2.8; patella L/W, 3.2/1.0; chela L/W/D, 5.4/1.5/1.3; fixed finger L, 3.0; movable finger L 3.4.

Variation.—*Vaejovis zapoteca* shows marked sexual dimorphism. Males with proportionately stouter pedipalps and longer metasomal segments, scalloping pronounced in the fingers of the pedipalp chela. Pectinal tooth count variation in Table 1. Sternite VII setae count (n = 39) 10 to 11 (mode = 10) Pedipalp finger dentition (n = 24): for the fixed finger, 24 fingers had 6 subrows of denticles; 24 fingers had 6 inner accessory denticles. For the movable finger, 24 fingers had 6 subrows of denticles. For the inner accessory denticles count we observed considerable variation between both chelae of a single specimen, so we counted both sides (n = 48): 1 × 6, 6 × 7, 31 × 8 (= mode), 9 × 9 and 1 × 10 inner accessory denticles. Telotarsus III distal spinule count (n = 39; one telotarsus broken): 4 with 3 (1 + 2), 29 with 4 (2 + 2), and 6 with 5 (2 + 3) spinules.

Morphometric ranges: Males (n = 11): Chela L/W, 2.77–3.28; patella L/W, 3.00–3.40; fixed finger L/chela L, 0.37–0.44; segment V L/W, 2.10–2.35; vesicle W/posterior margin of segment V, 1.46–1.67. Females (n = 10): Chela L/W, 3.60–4.73; patella L/W, 2.73–3.20; fixed finger L/chela L, 0.44–0.56; segment V L/W, 1.94–2.19; vesicle W/posterior margin of segment V, 1.17–1.36.

Distribution.—Known from the Northern Mountain range of Oaxaca (the Sierra Juarez) (Fig. 1).



Figures 30–36.—*Vaejovis dzahui* sp. nov. holotype male: 30. Right femur, dorsal view; 31. Right patella, dorsal view; 32. Right patella, retrolateral view; 33. Right chela, retrodorsal view; 34. Right chela, dorsal view; 35. Fixed finger, ventral view; 36. Metasomal segment V, ventral view. Scale bars = 0.5 mm.

Vaejovis dzahui sp. nov.
(Figs. 30–36)

Type data.—MEXICO: *Oaxaca*: holotype male, Distrito Coixtlahuaca, km 2 road San Cristobal Suchixtlahuaca – Santiago Tejupam (17°42.240′N, 97°23.667′W, elev. 2,290 masl), 28 June 2006, O. Francke, G. Villegas, H. Montaño and A. Valdez (CNAN-T0386). Paratypes: 5 males, 2 females, collected with holotype (CNAN-T0387); 4 males, 2 females, collected with holotype (AMNH).

Etymology.—The specific epithet is a Mixtec word meaning "rain" and it is used as a noun in apposition.

Diagnosis.—Adults 18–20 mm long. Base color yellow brown, with dark blackish markings on sternites. Pectinal tooth count on males 13–15 (mode = 14), on females 12–13 (mode = 12). Sternite VII with 10–15 setae (mode = 12). Metasomal segments short and wide, vesicle width/segment V posterior width mean = 1.09 (± 0.06) in males. Patella length/width mean = 2.72 (± 0.24) in males.

Vaejovis dzahui is similar to *V. franckei*, *V. setosus* and *V. pusillus* but it can be distinguished by the following: From *V. franckei* differs in: (1) Chela length/width on males ranges from 2.91–3.40 (2.56–3.00 on *V. franckei*); (2) Metasomal segment V length/width on males ranges from 0.35–0.44, whereas on *V. franckei* it ranges from 0.42–0.56; (3) Metasomal segment V length/depth on males ranges from 2.20–2.60, whereas on *V. franckei* it ranges from 1.75–2.00; (4) Fixed finger length/Chela length ranges from 0.42–0.56, whereas on *V. franckei* it ranges from 0.35–0.44.

From *V. setosus* differs in: (1) Patella length/width on males ranges from 2.50–2.71, whereas on *V. setosus* it ranges from 2.70–3.33; (2) Sternite VII with modal setae counts = 12, whereas on *V. setosus* it is 20; (3) *V. dzahui* is a smaller species than *V. setosus* (see Tables 1); (4) Pectinal tooth count mode on females = 12, whereas on *V. setosus* = 14.

From *V. pusillus* differs in: (1) Chela length/width on females ranges from 2.91–.40 in *V. dzahui*, whereas on *V. pusillus* it ranges from 4.00–4.10; (2) Pectinal tooth counts on females = 12–13, whereas on *V. pusillus* = 10–11 (mode = 11); (3) dorsolateral carinae on segment I flanked by one seta, whereas in *V. pusillus* lacks setae.

Description of holotype male.—*Coloration:* Base color yellow brown; with dark fuscous markings on tergites, metasoma and appendages; ventral aspect base color light yellow to light brown; sternites and pectines heavily mottled. Chelicerae with dusky markings limited to distal margins; cheliceral dorsal surface mostly cream yellow.

Prosoma: Anterior margin of carapace straight to weakly emarginated; surface around the median eyes densely, finely granulose, interspersed with scattered coarse granules.

Mesosoma: Tergites sparsely, coarsely granulose; shagreened. Tergites I–VI: median carina on I obsolete, on II–VI weak, granulose. Submedian carinae on I–II vestigial; on III–V weak, granulose; on VI moderate, granular. Tergite VII: median carina present on anterior two-thirds; submedian and lateral carinae strong, granular. Genital papillae well developed. Sternites III–VI smooth to shagreened medially, with dusky markings; sparsely setose. Sternite VII lateral carinae weak to faint, smooth to feebly granulose; submedian carinae absent. Sternite VII with 14 setae. Pectinal tooth count 14–14.

Metasoma: Segments I–IV: intercarinal spaces densely, coarsely granulose. Dorsolateral carinae on I strong, granular to crenulate; on II–IV strong, crenulate. Lateral supramedian carinae on I–III strong, crenulate; on IV strong, crenulate to granular. Lateral inframedian carinae on I strong, granular; on II present only on posterior half, strong, granular to serrate; on III present only on distal one-third, strong, serrate; on IV absent. Ventrolateral carinae on I moderate, irregularly crenulate; on II–IV strong, irregularly crenulate. Ventral submedian carinae on I obsolete; on II weak, granular; on III moderate, granular to crenulate; on IV strong, irregularly crenulate. Segment V: Dorsolateral carinae moderate, granular to crenulate; lateral carinae weak to moderate, granular; ventrolateral carinae strong, granular to crenulate; ventromedian carina moderate to strong, granular to crenulate. Intercarinal spaces densely, coarsely granular.

Telson: Vesicle wider than the posterior margin of segment V; ventral surface irregularly granulose, with 4 pairs of setae (Fig. 36).

Pedipalps: Orthobothriotaxic "C". Femur (Fig. 30): Dorsal surface densely, finely granulose with some coarse granulation. Prodorsal carina strong, granular to crenulate. Retrodorsal carina moderate to weak, granular. Proventral carina weak, granular. Retroventral carina weak to moderate, feebly granular. Setation (right/left): prodorsal with 4/3 setae, 3/3 medial setae on prolateral face; retroventral carinae with 2/2 setae. Patella (Figs. 31, 32) with retrodorsal carina obsolete; prodorsal carina moderate, crenulate to smooth; retroventral carina obsolete to faint, smooth; proventral keel weak, granular. Setation: 4/4 prodorsal setae. Chela (Figs. 33, 34) rounded, short. Digital, prodorsal and dorsal secondary carinae weak to vestigial, smooth; all other carinae obsolete. Fixed finger (Fig. 35) with primary row divided into six subrows by five enlarged primary row denticles; six inner denticles. Movable finger with primary row divided into six subrows by five enlarged primary row denticles; seven inner denticles.

Legs: Basitarsus I with two ventrosubmedian rows of spinules. Basitarsus II with one ventrosubmedian row of spinules, divided by 3 large setae. Basitarsus III–IV with one ventrosubmedian row of spinules, divided by 4 large setae. Telotarsus I–IV with one ventromedial row of spinules bifurcating distally, with four spinules (2 pro- and 2 retrolateral) on one leg and five spinules (2 + 3) on the other leg

Hemispermatophore: Lamelliform; hooks short, thick, basal; no sclerotized hemi-mating plug (Figs. 52, 53).

Measurements.—*Holotype male:* Total L, 18.2; carapace L, 2.5; mesosoma L, 5.8; metasoma L, 8.0. Metasomal segments: I L/W, 1.0/1.5; II L/W, 1.1/1.4; III L/W, 1.3/1.4; IV L/W, 1.7/1.3; V L/W/D, 2.9/1.2/1.1. Telson: Vesicle L/W/D, 1.9/1.0/0.8. Pedipalp: Total L, 7.1; femur L, 1.7; patella L/W, 2.0/0.8; chela L/W/D, 3.4/1.0/1.2; fixed finger L, 1.6; movable finger L, 2.0.

Paratype female: Total L, 19.3; carapace L, 2.5; mesosoma L, 7.9; metasoma L, 7.2. Metasomal segments: I L/W, 1.0/1.6; II L/W, 1.1/1.4; III L/W, 1.3/1.4; IV L/W, 1.5/1.2; V L/W/D, 2.3/1.2/1.2. Telson: Vesicle L/W/D, 1.7/1.1/0.7. Pedipalp: Total L, 7.5; femur L, 1.8; patella L/W, 2.1/0.8; chela L/W/D, 3.6/0.9/1.0; fixed finger L, 1.7; movable finger L, 2.1

Variation.—*Vaejovis dzahui* shows no marked sexual dimorphism, other than genitalia and pectines. Pectinal tooth count variation in Table 1. Sternite VII setae count ($n = 14$) 10 to 15 (mode = 12). There was no variation in the pedipalp chela finger dentition, all specimens have six subrows of denticles in both fingers; on the fixed finger all specimens have six inner accessory denticles, whereas the movable finger has seven. Telotarsus III distal spinule count ($n = 12$) two telotarsi with two (1 + 1), 12 with three (1 + 2), 9 with four (2 + 2) and one with five (2 +3) spinules.

Morphometric ranges: Males ($n = 10$): Chela L/W, 2.91–3.40; patella L/W, 2.50–2.71; fixed finger L/chela L, 0.42–0.56; segment V L/W, 1.86–2.42; vesicle W/posterior margin of segment V, 1.11–1.33. Females ($n = 4$): Chela L/W, 3.40–4.00; patella L/W, 2.63–3.14; fixed finger L/chela L, 0.42–0.47; segment V L/W, 1.92–2.20; vesicle W/posterior margin of segment V, 1.10–1.22.

Distribution.—This species is only known from the type locality (Fig. 1).

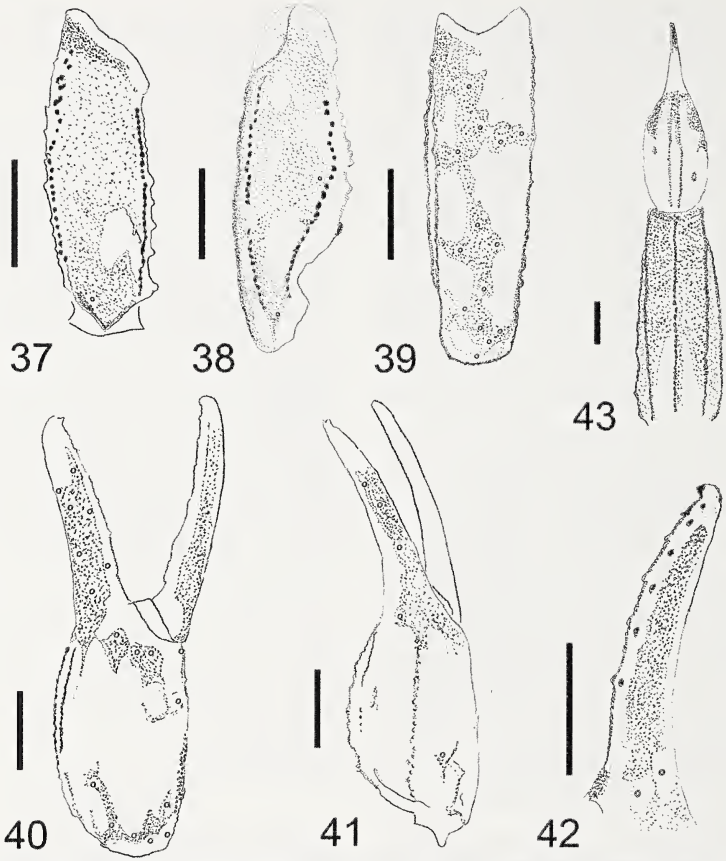
Vaejovis darwini sp. nov.
(Figs. 37–43)

Type data.—MEXICO: *Oaxaca*: Holotype male, Distrito Juquila, from 3 km west San Pedro Juchatengo (16°21.824′N, 97°06.584′W, elev. 845 masl), 27 June 2006, O. Francke, G. Villegas, H. Montaño, C. Santibáñez and A. Valdez (CNAN-T0388). Paratypes: 1 male, 1 female, collected with holotype (CNAN-T0389); 1 male, 1 female, collected with holotype (AMNH).

Etymology.—The specific epithet is dedicated to Charles Darwin in commemoration of the 200-year anniversary of his birth, and the 150th anniversary of the publication of "On the Origin of Species by Means of Natural Selection."

Diagnosis.—Adults 26–33 mm long. Pedipalp chela with dorsal marginal and prodorsal carinae moderate, granular; chela length/width mean = 3.91 (± 0.34) in males. All metasomal segments longer than wider; Segment V length/width mean = 2.58 (± 0.21) on males. Pectinal tooth count on males 17 ($n = 6$), on females 15–16 (mode = 16). Sternite VII with 11–12 setae.

Vaejovis darwini is similar to *V. nigrofemoratus*, *V. prendinii* and *V. zapoteca*; from *V. nigrofemoratus* differs in: (1) Pectinal tooth count on females = 15–16, whereas on *V. nigrofemor-*



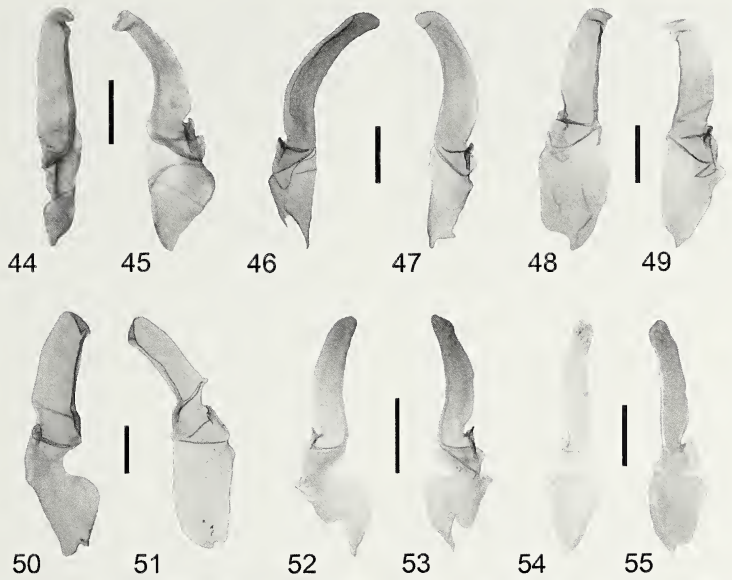
Figures 37–43.—*Vaejovis darwini* sp. nov., holotype male. 37. Right femur, dorsal view; 38. Right patella, dorsal view; 39. Right patella, retrolateral view; 40. Right chela, retrodorsal view; 41. Right chela, dorsal view; 42. Fixed finger, ventral view; 43. Metasomal segment V, ventral view. Scale bars = 1 mm.

atus = 10; (2) *V. darwini* is bigger than *V. nigrofemoratus* (Total length range = 25.0–31.1 mm against 23.60 of the holotype female, and only known specimen of *V. nigrofemoratus*); (3) Metasomal segment V length/width on females ranges from 2.25–2.58, whereas on the holotype of *V. nigrofemoratus* it is 1.88.

From *V. prendinii* it differs as follows: (1) Chela length/width on males ranges from 3.63–4.00, whereas on *V. prendinii* it ranges from 2.95–3.50; (2) Metasomal segment V length/width on males ranges from 2.53–2.81 (2.00–2.20 on *V. prendinii*); (3) Pectinal tooth count on males 17 and on females 15–16, whereas in *V. prendinii* on males = 18–20 and on females = 17–18; (4) Sternite VII setae count 11–12, mode = 12 (in *V. prendinii* = 20–23, mode = 22).

From *V. zapoteca* it can be separated by the following: (1) Vesicle width/metasomal segment V posterior margin width on males ranges from 1.00–1.17, whereas on *V. zapoteca* it ranges from 1.46–1.67; (2) Chela on adult males without scalloping in the fingers, whereas on *V. zapoteca* pronounced scalloping is present; (3) Pectinal tooth count on males = 17, whereas on *V. zapoteca* on males = 12–15 (mode = 13); (4) Femur darker on *V. darwini* than on *V. zapoteca*.

Description of holotype male.—*Coloration:* Base color yellow brown; with dark, fuscous markings on tergites, metasoma and appendages; ventrally base color light yellow to light brown; sternites heavily mottled. Chelicerae with dusky markings limited to distal margins; most of cheliceral dorsal surface cream yellow.



Figures 44–55.—Morphology of the hemispermatophores: 44. *Vaejovis setosus*, dorsal view (male from km 45.8 federal road 175, Oaxaca-Ixtlan de Juarez); 45. Same, ventral view; 46. *Vaejovis franckei*, dorsal view (male from 6 km W Llano Grande, San Antonio Cuajimoloyas); 47. Same, ventral view; 48. *Vaejovis prendinii*, dorsal view (paratype male from Rio Grande, San Juan Atepec, CNAN-T0378); 49. Same, ventral view; 50. *Vaejovis zapoteca*, dorsal view (paratype male from Puerta del Sol, San Pablo Macuiltianguis, CNAN-T0382); 51. Same, ventral view; 52. *Vaejovis dzahui*, dorsal view (paratype male from km 2 road San Cristobal Suchixtlahuaca – Santiago Tejupam, CNAN-T0387); 53. Same, ventral view; 54. *Vaejovis darwini*, dorsal view (paratype male from 3 km W San Pedro Juchatengo, CNAN-T0389); 55. Same, ventral view. Scale bars = 0.5 mm.

Prosoma: Carapace anteriorly weakly emarginated; surface around median eyes densely, finely granulose interspersed with scattered coarse granules. Entire surface moderately granulose.

Mesosoma: Tergites sparsely, coarsely granulose; shagreened. Tergites I–VI: median carina on I obsolete, on II–VI weak, granulose. Submedian carinae on I–II vestigial; on III–V weak, granulose; on VI moderate, granulose. Tergite VII: median carina present on anterior two-thirds, granular; submedian and lateral carinae strong, granular. Genital papillae well developed. Sternites III–VI smooth; sparsely setose. Sternite VII with submedian carinae weak granular; lateral carinae moderate, granular. Sternite VII with 12 setae, lateral carinae, with 12 setae. Pectinal tooth count 17–17.

Metasoma: Segments I–IV: intercarinal spaces weakly, coarsely granulose, shagreened. Dorsolateral carinae on I–IV strong, crenulate. Lateral supramedian carinae on I, strong, crenulate to granular; on II–IV strong, crenulate. Lateral inframedian carinae on I strong, granular; on II–III present only on distal one-third, moderate, granular; on IV absent. Ventrolateral carinae on I moderate, irregularly crenulate; on II strong, irregularly crenulate to smooth; on III–IV strong, crenulate to granular. Ventral submedian carinae on I weak to moderate, granular to crenulate; on II moderate, granular to crenulate; on III–IV strong, granular to crenulate. Segment V: Dorsolateral carinae moderate, granular to crenulate; lateral carinae present on proximal two-thirds and fading distally, weak to moderate, granular to crenulate; ventrolateral carinae strong, granular to crenulate; ventromedian carina strong, granular to crenulate. Intercarinal spaces sparsely, coarsely granulose, shagreened.

Telson: Vesicle wider than posterior margin of segment V; ventral surface irregularly granulose, with 2 pairs of setae (Fig. 43).

Pedipalps: Orthobothriotaxic "C". Femur (Fig. 37): Dorsal surface densely, finely granulose with some coarse granulation. Prodorsal carina strong, granular to crenulate. Retrodorsal carina moderate to weak, granular. Proventral carina moderate to weak, granular. Retroventral carina weak to moderate, feebly granular. Setation (right/left): prodorsal carinae with 4/3 setae, 2/2 medial setae on prolateral face; retroventral carina with 4/3 setae. Patella (Figs. 38, 39) with retrodorsal carina moderate to weak, granular to crenulate; prodorsal carina moderate, crenulate to smooth; retroventral carina weak, smooth to granular; proventral carina weak, granular. Setation (right/left): 6/6 prodorsal setae. Chela slender (Figs. 40, 41); dentate margins of fingers straight. Digital carinae moderate, granulose; prodorsal, dorsosecondary and retrolateral carinae moderate to weak, smooth; two prolateral carinae (dorsal and ventral) weak to moderate,

granulose; all other carinae obsolete. Fixed finger with primary row divided into six subrows by five enlarged primary row denticles; six inner denticles (Fig. 42). Movable finger with primary row divided into six subrows by five enlarged primary row denticles; seven inner denticles.

Legs: Basitarsus I with two ventrosubmedian rows of spinules. Basitarsus II with one ventrosubmedian row of spinules divided by 3 large setae. Basitarsus III–IV with one ventrosubmedian row of spinules divided by 4 large setae. Telotarsus I–IV with one ventromedial row of spinules bifurcating distally, with three spinules (1 pro- and 2 retrolateral) on one leg and four spinules (2 + 2) on the other leg.

Hemispermatophore: Lamelliform; hooks short, basal; lamella thick and straight; no sclerotized hemi-mating plug (Figs. 54, 55).

Measurements.—*Holotype male:* Total L, 27.1; carapace L, 3.8; mesosoma L, 7.6; metasoma L, 13.1. Metasomal segments: I L/W, 1.7/2.0; II L/W, 1.9/1.9; III L/W, 2.1/1.7; IV L/W, 2.9/1.6; V L/W/D, 4.5/1.6/1.6. Telson: Vesicle L/W/D, 2.6/1.4/1.2. Pedipalp: Total L, 12.4; femur L, 3.0; patella L/W, 3.6/1.1; chela L/W/D, 5.8/1.6/1.7; fixed finger L, 2.5; movable finger L, 3.4.

Paratype female: Total L, 12.9; carapace L, 3.9; mesosoma L, 11.5; metasoma L, 13.3. Metasomal segments: I L/W, 1.7/2.4; II L/W, 2/2.2.0; III L/W, 2.2/2.0; IV L/W, 2.9/2.0; V L/W/D, 4.5/2.0/1.8. Telson: Vesicle L/W/D, 2.4/1.6/1.2. Pedipalp: Total L, 12.9; femur L, 3.0; patella L/W, 3.8/1.2; chela L/W/D, 6.1/1.6/1.8; fixed finger L, 2.8; movable finger L, 3.4.

Variation.—*Vaejovis darwini* shows no marked sexual dimorphism other than genitalia and pectines. Pectinal tooth count variation in Table 1. Sternite VII setae count ($n = 5$) 11–12 (mode = 12). There was no variation in the pedipalp chela finger dentition, all specimens have six subrows of denticles on both fingers; on the fixed finger all specimens have six inner accessory denticles, whereas on the movable finger they have seven. Telotarsus III spinule count ($n = 5$) six with three spinules (1 + 2) and four with four spinules (2 + 2).

Morphometric ranges: Males ($n = 3$): Chela L/W, 3.63–4.00; patella L/W, 3.27–3.82; fixed finger L/chela L, 0.43–0.46; segment V L/W, 2.53–2.81; vesicle W/posterior margin of segment V, 1.00–1.17. Females ($n = 2$): Chela L/W, 3.81–4.47; patella L/W, 2.85–3.27; fixed finger L/chela L, 0.40–0.43; segment V L/W, 2.25–2.58; vesicle W/posterior margin of segment V, 1.07.

Distribution.—This species is only known from the type locality (Fig. 1).

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A new species of *Hadrobunus* (Opiliones: Sclerosomatidae: Leiobuninae) from the southeastern United States

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Abstract. A new species of harvestman from the endemic North American genus *Hadrobunus* Banks, 1900 is described. The species, *H. fusiformis*, differs substantially from known USA species in both somatic and genital morphology, but the male resembles that of *H. knighti* from northern Mexico in having a long, narrow penis and posteriorly tapered opisthosoma.

Keywords: Harvestmen, systematics, taxonomy

The genus *Hadrobunus* Banks 1900 is traditionally distinguished from other New World Leiobuninae by relatively short legs (i.e., femur I shorter than length of body) and minute, posteriorly curved (retrorse) spinules or acuminate to spinulate tubercles distributed on the dorsum, especially the scutum (Figs. 1, 2, 9, 11). Taxonomists have heretofore recognized four species. *Hadrobunus grandis* (Say 1921) and *H. maculosus* (Wood 1868) occur in the eastern United States, with *H. maculosus* ranging into southeastern Canada. Two species, *H. davisi* Goodnight & Goodnight 1942 and *H. knighti* Goodnight & Goodnight 1942, occur in Mexico. The two northern species have large bodies and robust legs as well as highly derived penes (Fig. 3) and female genital opercula (Fig. 4). They are now most often distinguished by ambiguous and somewhat arbitrary (largely geographic) criteria offered by Bishop (1949), and it is possible that current concepts of the two species are artifacts of taxonomic history. Indeed, Say probably described *Phalangium grandis* from material obtained during his 1817–1818 expedition to northeastern Florida and coastal Georgia (Bennet 2002), but the types were lost over 140 years ago. Consequently, all subsequent discussion of the species has occurred without clear knowledge of its type locality or details of its morphology, although it is generally assumed to be similar to *H. maculosus*. The Mexican species are distinct from one another and from the northern species, but each is known from one individual. *Hadrobunus davisi* is known from the female holotype. It is small (3.9 mm long), with very well-developed retrorse spination and an unremarkable genital operculum (Fig. 8). *Hadrobunus knighti* is known from the male holotype (female specimens appear to have been lost). It is large (8.3 mm long), with a long, sacculate penis (Fig. 7) similar to that of many other Leiobuninae.

While visiting the collection at the Academy of Natural Sciences in Philadelphia in 2007, I found a vial containing three specimens (two males and one female) representing an undescribed species of *Hadrobunus* from the mountains of western North Carolina. Subsequent examination of other collections revealed that the late Norman W. Davis (b.1905 - d. 1969) had recognized the species as new based on material collected in September 1930 by Theodore H. Hubbell. Davis never published his findings, although he labeled the specimens "*Hadrobunus fusiformis* Davis" and designated them all as "paratypes." They are now part of the "Cornell Collection" at the American Museum of Natural History. The new species differs substantially from its congeners in the United States and Canada, but is very similar to the Mexican *H. knighti* in both general body form and basic construction of the penis (Fig. 5), although the penis of the new species lacks the subterminal sacs of *H. knighti* (Fig. 7). Consequently, *Hadrobunus fusiformis* is an important addition to the harvestman fauna of eastern North America.

METHODS

All observations were conducted using a Leica MZ APO dissecting microscope (16× ocular, 0.63× objective, 8–80× zoom). Pencil drawings were made using a drawing tube, digitally scanned, and then traced and finished using Adobe Illustrator CS2 software.

The specimens examined for this study are lodged in the following depositories: Academy of Natural Sciences, Philadelphia (ANSP); American Museum of Natural History, New York (AMNH); Florida State Collection of Arthropods, Gainesville (FSCA); National Museum of Natural History (Smithsonian Institution), Washington D.C. (NMNH); North Carolina Museum of Natural Sciences, Raleigh (NCMNS); Texas Tech University Museum, Lubbock (TTUM); University of Maryland, J.W. Shultz Collection (UMD); and Virginia Museum of Natural History, Martinsville (VMNH).

Material examined.—*Hadrobunus maculosus:* USA: *Maryland*: Prince Georges Co., many ♂, many ♀, Beltsville, USDA Research Farm, 39.0244°N, 76.8987°W, 7 September 2006, L. Moore (UMD); Garrett Co., many ♂, many ♀, 6 km NW Westernport, COHO2 Managed Oak Forest, elev. 559 m, 39.508°N, 79.110°W, 12–19 August 2005, L. Morgens et al. (UMD). *Massachusetts*: Middlesex Co., 1 ♂, Groton, 42.6112°N, 71.5745°W, 18 August 1967, Chickering (MCZ 37037); 1 ♂, Lincoln, 42.4258°N, 71.3044°W, 27 July 1967, Chickering (MCZ 37035); 1 ♂, Pepperell 42.6658°N, 71.5889°W, August 1968, H. & L. Levi (MCZ 36347), 1 ♂, Pepperell, August 1963, H. Levi (MCZ 36345); 1 ♂, Pepperell, 27 August 1963, L. Levi (MCZ 36344); 1 ♂, Pepperell, June 1966, H.W. Levi (MCZ 36352); 1 ♀, Pepperell, August 1966, H.W. Levi (MCZ 36356); 1 ♂, 1 ♀, Sherborn, 42.2389°N, 71.3703°W, August [no year], A.P. Morse (MCZ 38518). *New York*: Dutchess Co., 2 ♀, Poughkeepsie, 41.7064°N, 73.9208°W, no date, no coll. (MCZ 36354). *North Carolina:*

Figures 1–2.—*Hadrobunus fusiformis* new species, dorsal perspectives: 1. Male (North Carolina, Buncomb Co., 8 km west of Ashville); 2. Female (North Carolina, Jackson Co., Pathertown Valley). Scale bar = 1 mm.

Alamance Co., 1 ♀, Burlington, 36.0897°N, 79.4455°W, 19 September 1935, HKW (MCZ 37144). *Pennsylvania*: Bucks Co., 1 ♀, Rushland, Wilkenson Road, Coyne Farm, vernal marsh on wooded hilltop, ex. Malaise trap, site 1, 40.2503°N, 75.0417°W, 21 July–5 August 1998, H. O'Connor (ANSP); 3 ♂, Rushland, Wilkenson Road, Coyne Farm, vernal marsh on wooded hilltop, ex. Malaise trap, site #1, 40.2503°N, 75.0417°W, 6–20 August 1998, H. O'Connor (ANSP). *Virginia*: Botetourt Co., many ♂, many ♀, Roaring Run, pitfall, 37.3923°N, 79.4157°W, 30 June 1996, M. Donahue & B. Hogan (VMNH). Augusta Co., many ♂, many ♀, George Washington National Forest, ~ 5 mi [~ 8 km] W of Stokesville, Comp. 460-3, Trap 3, 38.3606°N, 79.2589°W, 1 September 1989, B. Flamm (VMNH). *West Virginia*: Berkeley Co., many ♂, many ♀ (in many separate vials), Sleepy Creek Hunt & Fish Area, Third Hill Mtn., oak-pine forest, pitfall, 39.4387°N, 78.1944°W, many dates in 1985, P.J. Martinson (NMNH). Fluvanna Co., 5 ♂, 4 ♀, Kents Store, Bell drift fence site, 37.8793°N, 78.1289°W, 13 September 1995, M. Bell (VMNH).

Hadrobunus davisi: MEXICO: *Guerrero*: ♀ holotype, Acapulco, 16.87°N, 99.9°W, 17 June 1936, L.I. Davis (AMNH).

Hadrobunus knighti: MEXICO: *Nuevo León*: ♂ holotype, Villa de Santiago, Hacienda Vista Hermosa, Horsetail Falls [= Cascada Cola de Caballo], 25.3850°N, 100.1612°W, elev. 2500 ft [= 762 m], 16 June 1940, K. Knight (AMNH).

TAXONOMY

Family Sclerosomatidae Simon 1879
Subfamily Leiobuninae Banks 1893
Hadrobunus Banks 1900

Hadrobunus Banks 1900:199.

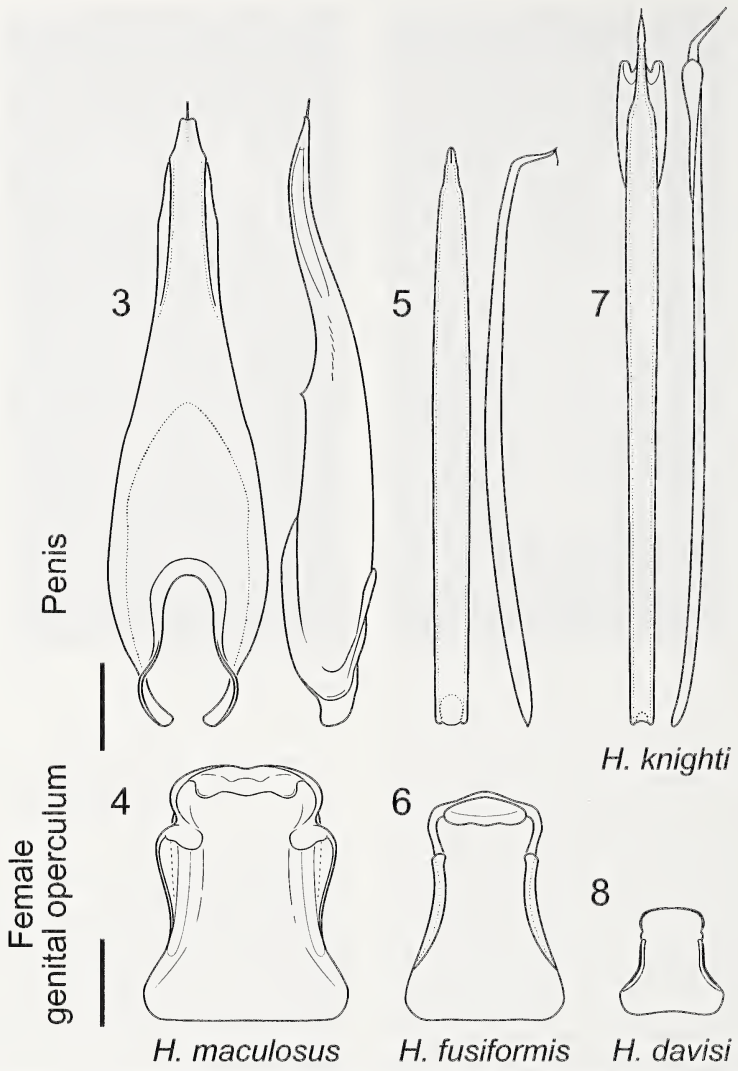
Type species.—*Phalangium grandis* Say 1821, by subsequent designation (Banks 1900).

Diagnosis.—Dorsum with minute, posteriorly curved (retrorse) spinules or acuminate to spinulate tubercles, especially numerous on propeltidium (especially on margins), meso- and metapeltidia and anterior tergal bands of scutum. Legs relatively short: femur I subequal to length of body or shorter. Ocularium weakly canaliculate or not canaliculate; each carina with a row of denticles. Retrolateral row of denticles absent or much reduced on coxa III.

Hadrobunus fusiformis new species
Figs. 1, 2, 5, 6, 9–16

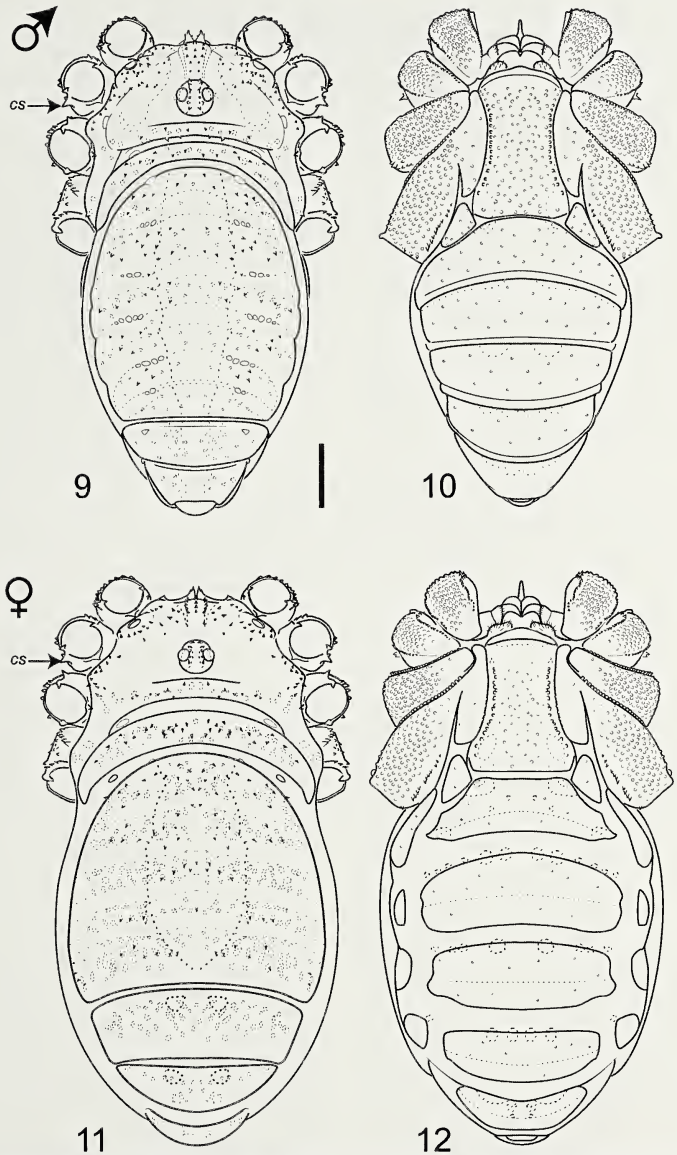
Types.—USA: *North Carolina*: Swain Co., ♂ holotype, Smokemont, Great Smoky Mountains National Park, 35.5141°N, 83.3024°W, 5 August 1939, Rehn & Rehn (ANSP). Paratypes: 1 ♀, same data as holotype (ANSP), 1 ♂, same data as the holotype (NMNH).

Other material examined.—*Georgia*: Camden Co., 6 ♂, 2 ♀, 30.92°N, 81.64°W [estimated from county center], 25 Septem-

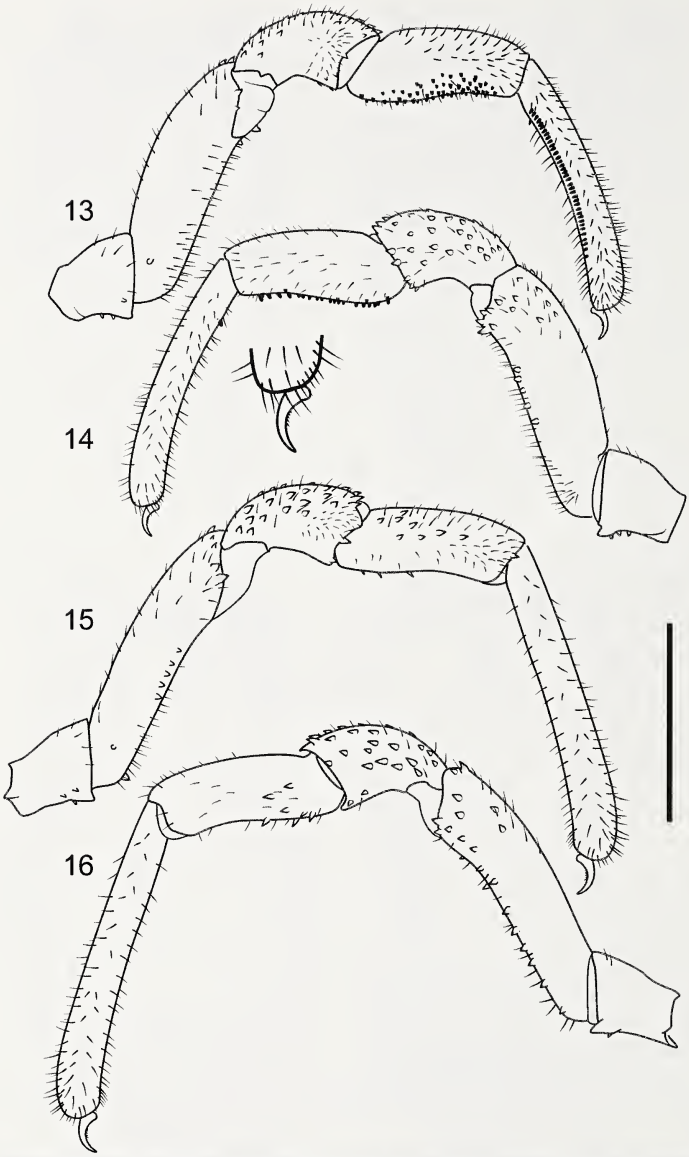


Figures 3–8.—Comparison of genital structures of known species of *Hadrobunus*. Penes illustrated with dorsal perspective on left and lateral perspective on right, with right side of lateral view corresponding to dorsal surface. Female genital opercula from internal (dorsal) perspective; flexible inner cuticle and sheath of ovipositor removed. All figures to same scale. Scale bars = 1 mm.

ber 1930, T.H. Hubbell [vial labeled "PARATYPE: *Hadrobunus fusiformis* Davis" by N.W. Davis] (AMNH). Habersham or Ruben Co., 1 ♂, Tallullah Falls, 34.7368°N, 83.3751°W, 30 July 1909, J.C. Bradley [vial labeled "PARATYPE: *Hadrobunus fusiformis* Davis" by N.W. Davis] (AMNH). Liberty Co., 2 ♂, 1 ♀, Midway, 31.8058°N, 81.4307°W, 30 September 1930, T.H. Hubbell [3 vials labeled "PARATYPE: *Hadrobunus fusiformis* Davis" by N.W. Davis] (AMNH). *North Carolina*: Buncomb Co., 1 ♂, 5 mi [8 km] W Ashville, Rte. 23/19, vacant lot, 35.5345°N, 82.7106°W, 17 July 1961, S & D Mulaik (AMNH). Buncomb or Haywood Co., 1 ♂, 1 ♀, Mount Pisgah, elev. 4000–5000 ft [1219–1524 m],



Figures 9–12.—*Hadrobunus fusiformis* new species: 9. Male holotype, dorsal view; 10. Male holotype, ventral view (setae not depicted); 11. Female paratype, dorsal view; 12. Female paratype, ventral view (setae not depicted). Abbreviation: *cs*, coxal spur. All figures to same scale. Scale bar = 1 mm.



Figures 13–16.—*Hadrobunus fusiformis* new species, left palps (recumbent microsetae not depicted): 13. Male holotype, prolateral view; 14. Male holotype, retrolateral view; inset (2×) showing armament of claw; 15. Female paratype, prolateral view; 16. Female paratype, retrolateral view. All figures to same scale. Scale bar = 1 mm.

under rocks, 35.4255°N, 82.7569°W, 5 July 1959, P. Weems (FSCA), 11 ♂, 4 ♀, H.V. Weems, Jr. [2 vials] (FSCA). Jackson Co., 1 ♂, Gribble Gap, 35.3079°N, 83.2082°W, ? July 1971, F. Coyle (TTUM: TTU-Z 58,766); 1 ♀, Pathertown Valley, 35.3265°N, 83.1220°W, 7 August 2000, J.C. Cokendolpher (TTUM: TTU-Z 58,679). Macon Co., 2 ♀ penult., Coweeta Hydrologic Station, 35.0596°N, 83.4205°W, 30 June 1978, L. Reynolds (NCMNS A6976); 1 ♂, 1♀, 15 August 1977 (NCMNS: A6811); 4 ♂, 18 August 1978 (NCMNS: A6904 & A6905); 1 ♀, 22 August 1977 (NCMNS: A6855); 1 ♀, 25 August 1977 (NCMNS: A7259), 1 ♀, 8 September 1978 (NCMNS: A7240); 2 ♂, 15 September 1978 (NCMNS: A6948 & 6944); 1 ♀, 22 September 1977 (NCMNS: A6865). Transylvania Co., 1 ♂, 3.2 mi [5.1 km] NNW Brevard, US 276, 4.9 mi [7.9 km] N US 64, 35.3098°N, 82.6161°W, 29 August 1973, R.W. Shelley (NCMNS: 1981). *South Carolina*: Aiken Co., 1 ♂, 1 ♀, 15 mi [24 km] SW Aiken, 33.4051°N, 81.8901°W, 15 September 1983, L. Robbins (TTUM: TTU-Z 58,808); 11 ♂, 23 ♀. Beaufort Co., Hardeeville, 32.2871°N, 81.0807°W, 29 September 1930, T.H. Hubbell [3 vials labeled "PARATYPE: *Hadrobunus fusiformis* Davis" by N.W. Davis] (AMNH). Colleton Co., 19, 22, Round O, 32.9396°N, 80.5441°W, elev. 11 m, 29 Sept. 1930, T.H. Hubbell [7 vials labeled "PARATYPE: *Hadrobunus fusiformis* Davis" by N.W. Davis] (AMNH).

Etymology.—The late Norman W. Davis recognized the species described here as new, but he did not publish a description. Davis used the specific epithet *fusiformis* on his labels, a name that acknowledges the unusual fusiform shape of the male body. Davis's name is retained here.

Diagnosis.—Penis long (87% body length), linear, simple, without sacs, dorsoventrally compressed throughout; intrinsic penial muscle pinnate, with short fibers attaching along full length of shaft (Fig. 5). Posterior end of male opisthosoma extended, somewhat pointed, giving the body a fusiform appearance (Figs. 1, 9, 10). Male palpal tibia with broad field of dark peg-like spines on ventral and proventral surfaces (Figs. 13, 14). Male scutum with six tergites (Figs. 1, 9). Female genital operculum (Fig. 6) with large, heavily sclerotized anterior sclerite, lateral apodeme lacking anterior apophysis of female *H. maculosus* (Fig. 4).

Description.—*Male (holotype):* Body length, 7.4 mm; max. carapace width, 3.5 mm.

Dorsum (Figs. 1, 9): Cuticle finely granulate. Propeltidium with low, marginal preocular mound bearing one median and two lateral longitudinal rows of four or six sharp, conical spinules; rows extending more than halfway to ocularium. Marginal and submarginal regions of propeltidium, including mound of ozopore, with scattered sharp, dark, curved spinules. Supracheliceral lamina with pointed, divergent processes, each with two lateral spinules. Ocularium not canaliculate, each carina with highly irregular row of variably developed denticles (seven on the right, five on the left). Mesopeltidium with a few small, curved, dark spinules. Metapeltidium with scattered dark spinules and a few tubercles, tubercles concentrated laterally. Opisthosomal scutum composed of six fused tergites. Scutum and two free tergites with scattered small, dark, recurved spinules and rounded tubercles, some tubercles bearing spinules. Spinules most densely distributed on first two and last scutal tergites.

Venter (Fig. 10): Cuticle finely granulate. Lateral surfaces of coxae I–IV covered in low, rounded, circular tubercles, interspersed with erect macrosetae. Coxal denticles terminating in either a flat blade, a single median point or three points (large median point subtended by smaller point on either side). Long, well-defined rows of well-developed denticles present on prolateral surfaces of coxa I–IV and retrolateral surface of coxa IV. Row of denticles and/or denticle-like tubercles on retrolateral surface of coxa I, extending from distal end proximally three-fourths the length of the coxa. Row of conical tubercles on retrolateral surface of coxa II running from distal end proximally about half the length of the coxa. Retrolateral surface of coxa III without row of denticles or modified tubercles. Coxa I with retrolateral distal coxal spur (specialized denticle or denticles dorsal to coxa-trochanter articulation) consisting of one large point; coxa II with retrolateral distal spur with one large and one small point (Fig. 9: *cs*); coxa III without spurs but with prolateral prominence bearing last two slightly enlarged denticles of the prolateral row; comparable structure evident on coxa IV but not as well developed. Labrum simple, thin, elongate; terminus pointed.

Genital operculum: Broad, transversely convex; surface with low, rounded tubercles; scattered erect setae, especially anteriorly; laterally with submarginal, imperfect row of denticles; anterior margin rebordered, lip narrow, with slight anterior projection, lacking large, dark sclerite present in female.

Sternites: Finely granulate with scattered, low, rounded tubercles and fine, erect setae. Lateral portions of sternites completely or partly separated by thin line of flexible cuticle forming pleurites.

Chelicerae: Smooth except for erect macrosetae on dorsal surfaces of first and second articles, with cluster at base of fixed finger; short, peg-like spine projecting medially from base of fixed finger just distal to setal cluster.

Palps (Figs. 13, 14): Measurements (in mm): femur, 1.5; patella, 0.8; tibia, 1.0; tarsus, 1.6. Trochanter with a few scattered, erect setae dorsally and ventrally; distal retroventral apophysis robust, conical; several stout, sharp-tipped spines on and around apophysis. Femur with longitudinal series of stout conical spines along middle third of retroventral surface; distal retrolateral surface with cluster of large, thorn-like spines. Ventral surface with numerous erect setae and two small, stout spines. Dorsal surface with an imperfect prolateral longitudinal row of erect setae; distal one-fourth of dorsal surface with scattered erect setae and thorn-like spines, spines tending to be larger distally. Retrolateral surface largely smooth, with a few scattered setae; one proximal dark tubercle; two thorn-like spines at distal margin. Patella with large thorn-like spines on dorsal and retrolateral surfaces and distal prolateral margin, spines interspersed with scattered erect macrosetae; prolateral and ventral surfaces without spines but with erect macrosetae. Tibia with scattered erect macrosetae on most of surface (absent on proximo-prolateral surface); coat of distally recumbent microsetae present dorsally; ventral and proventral surface covered in short, dark, peg-like spines. Tarsus coated in distally recumbent microsetae and scattered macrosetae; proventral surface with file of 37 peg-like spines; proximal retroventral surface with

single peg-like spine. Claw with ventral series of five small teeth increasing in length distally.

Legs: Measurements of femur, patella, tibia, basitarsus and telotarsus (in mm): I: 4.6, 1.3, 3.7, 4.6, 6.7; II: 7.7, 1.5, 6.6, 6.9, 12.5; III: 4.8, 1.4, 3.5, 5.3, 6.5; IV: 7.3, 1.5, 5.2, 8.7, 8.9. Trochanters with compressed thorn-like spines on pro- and retrolateral surfaces, a few smooth tubercles on pro- and retrodorsal surfaces; dorsal and ventral surfaces essentially smooth. Femora proximal to annular constriction with small thorn-like spines dorsally and small tubercles ventrally; shaft with numerous distally pointing, thorn-like spinules grading from larger dorsally to minute ventrally. Similar thorn-like spinules on patellae and tibiae; tibial spinules decreasing in size and density distally; basitarsus IV with a few spinules on proximal dorsal surface. Tibiae, basitarsi, and telotarsi coated with recumbent microsetae, increasing in density distally. Basi- and telotarsi with scattered erect setae, increasing in length and density distally.

Penis (Fig. 5): Length, 6.5 mm. Shaft dorsoventrally flattened over most of length, slightly inflated proximally; well sclerotized, smooth; no sacs, bulbs, or alae. Glans held at about 100 degree angle to shaft, dorsoventrally flattened, tapering distally in lateral perspective, rounded terminus in dorsal perspective; two pairs of small, procurved spines projecting from lateral margin; stylus sinuate, angled posteriorly, arising from superior terminal margin of glans.

Coloration: From specimen stored over 70 years in ethanol; cuticle darkened and contrast reduced. Dorsum with dark brown background. Propeltidium with some light brown mottling, lateral margins darker; a few light spots on posterolateral surface. Light stripe arising anteriorly on each side of preocular mound, passing posteriorly and converging slightly toward midline but diverging from midline halfway to ocularium, continuing laterally to end at ocularium. Ocularium very dark brown basally, with light median band dorsally. Meso- and metapeltidium with imperfect transverse rows of light spots; cuticle darker medially than laterally, appearing as continuation of median scutal band. Opisthosomal scutum with dark median band ("saddle"); gradually broadening posteriorly, reaching greatest width on fourth scutal tergite, then narrowing gradually to the end of scutum, trace of saddle evident on first free opisthosomal tergite; no large, paired, dark spots as in female. Opisthosomal scutum crossed by six transverse bands of light spots separated by bands without spots; spots not as distinct as in female, nor arranged in small stripes on posterior part of scutum. Free tergites with a few light spots, especially laterally.

Venter: Pedal coxae broadly mottled with light and dark brown. Genital operculum light yellow-brown, brown at postero-lateral surface. Postgenital sternites uniformly brown, anterior margin of each sternite with bilaterally symmetrical band or row of dark brown spots indicating muscle attachments. Soft conjunctival cuticle light yellow-brown.

Chelicerae. Uniformly yellow-brown with darker chelal fingers.

Palps. Trochanter and proximal half of femur yellow-brown. Patella and distal portion of femur brown. Tibia light brown proximally, lightening distally. Tarsus yellow-brown.

Legs. Trochanters light brown on dorsal and ventral surfaces but dark on prolateral and retrolateral surfaces. Femora dark proximal to basal circumfemoral constriction, a light band just distal to constriction; remainder of femur brown. Patellae mottled with white and dark brown dorsally, homogenously light brown ventrally. Tibiae light brown proximally, brown distally with both darker and lighter mottling. Basitarsi and telotarsi yellow-brown, except for darker band at base of basitarsus and at articulations.

Female (paratype): Body length, 9.4 mm; max. carapace width, 3.9 mm.

Dorsum (Figs. 2, 11): Cuticle finely granulate. Propeltidium with low, marginal preocular mound bearing one median and two lateral longitudinal rows of four to six sharp spinules; rows extending less than halfway to ocularium. Marginal and submarginal regions of propeltidium, including mound of ozopore, with scattered sharp, dark, curved spinules. Anterior projections of supracheliceral lamina pointed, not diverging, with one or two lateral spinules. Ocularium not canaliculate, each carina with regular row of stout, curved denticles (five on the left, four on the right). Mesopeltidium with a few small, dark, curved spinules, separated from metapeltidium by wide band of conjuctival cuticle. Metapeltidium with scattered dark, curved spinules and a few tubercles, the latter concentrated laterally. Opisthosomal scutum composed of five fused tergites. Scutum and three free tergites of opisthosoma with scattered small, dark, recurved spinules. Spinules most densely distributed on anterior scutal tergites.

Venter (Fig. 12): Cuticle finely granulate. Lateral surfaces of coxae I–IV covered in low, rounded, circular tubercles, interspersed with erect setae. Well-defined rows of well-developed denticles present on prolateral surfaces of coxae I–IV and retrolateral surface of coxa IV. Denticles absent on retrolateral surface of coxae I and II, although marginal retrolateral tubercles larger and sharper, forming apparent row extending along distal half of coxa; marginal retrolateral tubercles on coxa II less developed than on coxa I. Retrolateral surface of coxa III without denticles or retrolateral row of modified marginal tubercles. Coxa I with retrolateral coxal spur consisting of one large point; coxa II with retrolateral spur with one large and one small point; coxa III without spurs but with prolateral prominence bearing last two slightly enlarged denticles of the prolateral row; comparable structure evident on coxa IV but not as well developed. Labrum simple, thin, elongate.

Genital operculum (Fig. 12): Covered externally with low, rounded tubercles; laterally with submarginal, imperfect row of denticles. Anterior margin rebordered, forming wide lip with slight anterior projection; submarginal sulcus well developed, darkened. Inner (dorsal) anterior surface with large, dark, smooth, reniform sclerite (Fig. 6).

Supra-opercular sternum with anterior and posterior regions. Anterior region typical, formed by free, transverse sclerite projecting anteroventrally just posterior to labium; distal free margin procurved with thin lateral projections bracing posterior surface of coxapophysis II. Posterior part heavily sclerotized, projecting posteriorly as part of dorsal wall of pregenital chamber, apparently fitting into corresponding parts of opercular sclerite. Sternites finely granulate, free lateral portions forming subrectangular pleurites, widely separated from sternites by flexible cuticle.

Chelicerae: Smooth except for erect setae on dorsal surfaces of first and second segments, with cluster at base of fixed finger.

Palps (Figs. 15, 16): Measurements (in mm): Femur, 1.6; patella, 0.8; tibia, 1.0; tarsus, 1.6. Trochanter with simple conical, disto-ventral apophysis and three short, stout ventral spines. Femur with longitudinal series of stout conical spines on retroventral surface interspersed with erect setae; spines shorter, more robust proximally. Dorsal surface with one or two imperfect longitudinal rows of setae; disto-dorsal, prolateral and retrolateral surfaces with small, low thorn-like spines, broad basally with sharp, black distal tip. Proventral surface with row of five short spines and one proximal tubercle. Patella with large thorn-like spines on dorsal and retrolateral surfaces and distal prolateral margin, spines interspersed with scattered erect setae; prolateral and ventral surfaces without spines but with erect setae; setae particularly dense on distal prolateral prominence (reduced patellar apophysis). Tibia with a longitudinal prolateral series of spines, more spines proximally but terminating with large distally projecting spine at terminal margin; a few spines along retroventral surface and proximally on retrolateral surface; otherwise with distally recumbent microsetae and erect macrosetae. Tarsus without spines, covered in micro- and macrosetae. Claw with ventral series of five teeth increasing in length distally.

Legs: Measurements of femur, patella, tibia, basitarsus, telotarsus (in mm): I: 4.5, 1.3, 3.4, 4.5, 6.4; II: 7.4, 1.5, 3.8, 4.8, 14.3; III: 4.7, 1.5, 3.8, 4.8, 6.3; IV: 7.5, 1.6, 5.2, 8.7, 9.6. Trochanters with compressed thorn-like denticles on pro- and retrolateral surfaces, dorsal and ventral surfaces essentially smooth. Small spinules on femora, patellae and proximal tibiae.

Coloration: From specimen stored over 70 years in alcohol; cuticle likely darkened and contrast reduced. Dorsum with dark brown background. Propeltidium with some light brown mottling, lateral margins darker; a few light spots on posterolateral surface. Light stripe arising anteriorly on each side of preocular mound, passing posteriorly and converging toward midline but terminating before reaching ocularium. Ocularium dark around lenses; concolorous with propeltidium anteriorly and posteriorly; light median band dorsally. Meso- and metapeltidium with imperfect transverse rows of light spots. Scutum with dark median band ("saddle") with lateral margins somewhat darker than center; broadens slightly posteriorly but narrows rapidly within last scutal tergite. Opisthosomal scutum crossed by five transverse bands of light spots separated by bands without spots; spots on last scutal tergite elongated or arranged longitudinally, giving the impression of many short stripes. First and second free tergites of opisthosoma with broad bands of small, elongated light spots anteriorly, no spots posteriorly; each tergite with large dark, irregular spot suggesting continuation of saddle. Last free tergite darker than preceding tergites, with light antero-median region and a few irregular light patches.

Venter. Pedal coxae broadly mottled with light and dark brown. Genital operculum light yellow-brown but brown within submarginal sulcus and at postero-lateral surface; internal marginal sclerite very dark brown. Postgenital sternites with brown and yellow-brown mottling but divided transversely into distinct anterior and posterior parts, with anterior being lighter than posterior. Anterior margin of each sternite with bilaterally symmetrical row of dark brown spots indicating muscle attachments. Pleural sclerites (detached lateral ends of sternites) without transverse separation as present in sternites but dark brown at lateral ends. Soft conjunctival cuticle light yellow-brown.

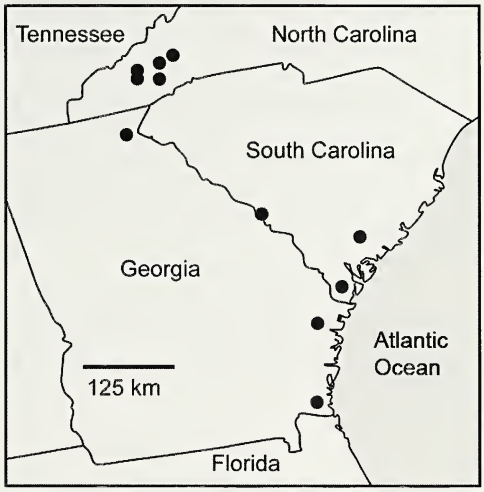


Figure 17.—Known collection sites for *H. fusiformis* new species.

Chelicerae. Uniformly yellow-brown with darker chelal fingers.

Palps. Trochanter uniformly light brown. Femur and patella with dark brown and light mottling on most surfaces but homogenously brown ventrally. Tibia light brown, homogeneous. Tarsus light yellow-brown, homogenous.

Legs. Trochanters concolorous with dorsum on dorsal and ventral surfaces but dark on prolateral and retrolateral surfaces. Femora dark proximal to basal circumfemoral constriction, a narrow light band just distal to constriction; remainder of femur brown though darker dorsally. Patellae mottled with white and dark brown dorsally, homogenously light brown ventrally. Tibiae with brown and whitish mottling dorsally, forming imperfect longitudinal stripes; more homogenous ventrally, without whitish component. Basitarsi and telotarsi yellow-brown, except for darker band at base of basitarsi and at articulations.

Distribution.—*Hadrobunus fusiformis* is known from the Blue Ridge Mountains of North Carolina and Georgia, near the Atlantic coast of South Carolina and Georgia and from one intermediate locality near Aiken, South Carolina (Fig. 17). This disjunct distribution is probably an artifact of sampling effort, and the species may occur widely in South Carolina and eastern Georgia.

COMMENTS

The paucity of diagnostic characters for *Hadrobunus* and the significant genitalic diversity of its constituent species (Figs. 3–8) invites speculation about the validity of the genus. However, in the absence of a taxonomic revision informed by

phylogenetic analysis, it would be premature to conclude that *Hadrobunus* is poly- or paraphyletic or that it should be divided into multiple genera. Indeed, a recent survey of museums and other collections by the author has revealed at least 10 undescribed species of *Hadrobunus* from the eastern and central United States. The emerging spectrum of morphological diversity in *Hadrobunus* also encompasses several species currently placed in *Leiobunum*. A much clearer picture of the diversity and phylogeny of *Hadrobunus* is required before taxonomic rearrangements are warranted. However, even among the undescribed species of *Hadrobunus*, *H. fusiformis* is distinctive and appears to have a unique position close to the Mexican *H. knighti*.

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SHORT COMMUNICATION

Sex differences in early instar behavior in *Pholcus phalangioides* (Araneae: Pholcidae)

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Abstract. Intersexual differences in juvenile behavior in invertebrates are poorly understood despite the recognition that they may be widespread. We present a study designed to explore sex differences in behavior in early instar long-bodied cellar spiders *Pholcus phalangioides* (Fuesslin 1775). Our findings reveal that sex differences in activity and feeding are present early in *P. phalangioides*, which may have important implications for studies of behavior that involve juveniles. Further investigation of the factors that underlie the early emergence of sex differences in behavior is needed.

Keywords: Juvenile, sex difference, behavior, cellar spider

Sex differences in adult behavior have been widely studied and are often ascribed to factors related to sexual selection including anisogamy (Bateman 1948), inequities in parental investment (Trivers 1972), and operational sex ratio (Emlen & Oring 1977) (Davies 1991; Andersson 1994). Significantly less is known about juvenile sex differences in behavior, despite recognition that they are likely to be prevalent for many reasons. For example, juvenile sex differences in behavior may emerge as consequences of sex-specific relationships among growth, survival, and fitness (Johnsson et al. 2001), as side-effects of sexually selected gene activity that promotes sexual differences in adults (Cheverud et al. 1983; Bakker 1996), or developmental programs that produce gradual changes in behavior instead of abrupt changes during sexual maturation (Williams 1992). Mammals and birds have received the greatest attention in studies of juvenile sex differences in behavior, and most of these studies have concentrated on play fighting (e.g., Eaton et al. 1986; Biben 1998; Paukner & Suomi 2008; Raihani et al. 2008). Only scarce attention has been paid to invertebrates in studies of juvenile sex differences in behavior (e.g., Singer & Riechert 1994; Persons 1999), and results from these few investigations are sometimes difficult to interpret. For example, Stevens et al. (2006) discovered sex differences in juvenile dispersal in corophiid amphipods, however they could not ascertain if sex differences were behavioral per se or artifacts of other factors.

We report an investigation exploring behavioral sex differences in early instar long-bodied cellar spiders *Pholcus phalangioides* (Fuesslin 1775). *P. phalangioides* is a cosmopolitan species strongly associated with human habitation. Hatched juveniles develop into adults after approximately 100 days and five molts (Uhl et al. 2004). Sexual dimorphism in this species is minimal, and in some populations, males are slightly larger than females (Uhl 1994). In the current investigation, we quantified the amount of time that early instar juveniles spent active in novel environments as well as the number of prey they consumed in a 24-h period. Once spiders matured and sex could be unambiguously assigned, we determined if there were sex differences in their juvenile behaviors. Voucher specimens were deposited in the Arcadia University insect collection.

In our investigation, we used juveniles that were second or third instar offspring of laboratory-raised adults that we originally collected from Pearson Hall at Miami University (Oxford, Butler County, Ohio, USA). We separated juveniles from their mothers after they molted to the second instar and maintained them individually in 5.5 cm high × 5.5 cm diameter clear, cylindrical, plastic containers. We fed juveniles two vestigial-winged *Drosophila melanogaster* once a week and housed them in a laboratory at Arcadia University (Glenside, Montgomery County, Pennsylvania, USA) with a relative humidity ~ 60%, a photoperiod of 12L:12D, and a temperature of approximately 25° C. Following the conclusion of all test trials, we raised juveniles to adulthood, switching their diets from *D. melanogaster* to two domestic crickets (2–6.35 mm; *Acheta domesticus*) once a week. Following maturation, we sexed all spiders.

We randomly assigned 59 juveniles (mean days post-molt = 4 days ± 0.82 SD) to one of two treatment groups: activity or foraging. We placed juveniles assigned to the activity group (n = 29) individually into unused plastic containers (described above) for a period of 15 min. Using stopwatches during live trials, we recorded the amount of time that each juvenile spent active during this period. An "active" spider was a spider moving any part of its body or its entire body. We did not discriminate between different types of activities (e.g., walking, web-building, etc.). Because the amount of time that juveniles spent active was not normally distributed, we made statistical comparisons between the sexes using a nonparametric Mann-Whitney U Test.

We did not offer juveniles assigned to the foraging group (n = 30) prey 24 h before trials commenced. To conduct a trial, we placed 10 vestigial-winged *D. melanogaster* with a juvenile spider in its home enclosure, and we recorded the number of flies that were consumed after a period of 24 h. Following sex assignment, we compared the number of flies consumed by the sexes using a two-sample t-test. We used JMP™ 5.1.2 statistical software to conduct all analyses.

We discovered statistically significant sex differences in both activity and foraging in early instar *P. phalangioides*. Juvenile males were significantly more active in enclosures than females (Mann-Whitney U Test, Z = 3.68, P = 0.0002, n = 29, Fig. 1), and juvenile females consumed significantly more flies in a 24 hr period than males (t ratio = 2.96, P = 0.007, n = 30, Fig. 2).

The results of our study suggest that sex differences in activity and feeding emerge early in *P. phalangioides*, and to our knowledge, this is a very rare documentation of juvenile sex differences in behavior in an invertebrate and in a spider. Our results have important implications for behavioral studies of spiders and perhaps other arthropods that include juveniles, as biased offspring sex ratios may confound the interpretation of results. For example, female biased sex ratios are common in social spiders, which have precise control of offspring sex ratio (Avilés 1986, 1993; Avilés et al. 1999, 2000). One species of solitary spider has been reported to have a female-biased sex ratio (Gunnarsson & Andersson 1992; Gunnarsson et al. 2004), and we

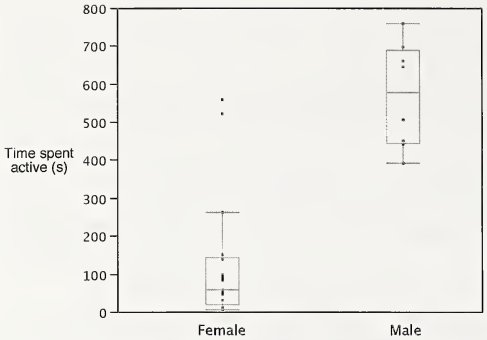

Figure 1.—The amount of time that early instar male (n = 8) and female (n = 21) *P. phalangioides* spent active in plastic enclosures. Box plots show lower and upper quartiles, and lines across boxes identify the median sample value.

have discovered female-biased, offspring sex ratios in *P. phalangioides* (Rypstra & Hoefler unpubl. data). For behavioral studies of species such as these and others, behaviors unique to the majority sex will be overrepresented in analyses if juvenile sex is not considered.

The reasons why *P. phalangioides* exhibit sex differences in juvenile behavior is not presently known, however several factors may be wholly or partially responsible. One possible explanation is that the intersexual differences discovered in our study are a result of an early divergence in developmental programs for males and females, whieh gradually prepares them for different roles during the reproductive phase of the life cycle. Historically, behavioral differences attributed to sex in spiders include active male dispersers that feed infrequently and sedentary females that feed often (Foelix 1996). Because *P. phalangioides* do not disperse by ballooning (Schäfer et al. 2001), the higher activity of males may be a reflection of male-biased dispersal and a result of selection favoring inbreeding avoidance (Bonte 2009). Similarly, through scramble competition, sexual seleetion may favor adult males that are able to locate and fertilize multiple females quickly (Andersson 1994), and this quality of high activity may develop early and gradually. The greater incidence of feeding by juvenile females may be a result from a correlated response to fecundity selection promoting higher feeding rates in adult females (Fox & Czesak 2000). To gain a clearer understanding of these possible underlying explanations, future studies should consider intersexual differences during successive ontogenetic stages.

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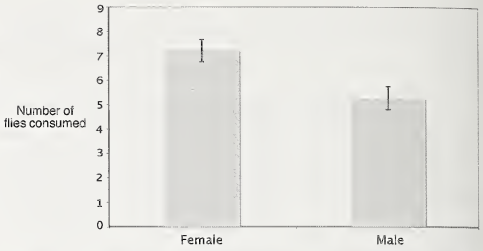

Figure 2.—The mean number of flies consumed ± SE by juvenile male (n = 11) and female (n = 19) *P. phalangioides*.

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SHORT COMMUNICATION

Benzoquinone-rich exudates from the harvestman *Pachylus paessleri* (Opiliones: Gonyleptidae: Pachylinae)

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Abstract. The chemical composition of the scent gland secretion of *Pachylus paessleri* Roewer 1913, a pachyline harvestman, was analysed by gas chromatography–mass spectrometry. The secretion is a six-component mixture of benzoquinones, with 2,3-dimethyl-1,4-benzoquinone and 2,3,5-trimethyl-1,4-benzoquinone being the main components (together amounting for ¾ of the secretion). Minor components are 2,5-dimethyl-1,4-benzoquinone (about 12%), 2-ethyl-3-methyl-1,4-benzoquinone (about 8%), 2,5-dimethyl-3-ethyl-1,4-benzoquinone (5%), and 2-ethyl-5-methyl-1,4-benzoquinone (about 1%). No sex-dependent differences could be detected. While dimethyl- and trimethyl-benzoquinones are widespread in scent gland secretions of Gonyleptoidea, 2,5-dimethyl-3-ethyl-1,4-benzoquinone and 2-ethyl-5-methyl-1,4-benzoquinone are reported for the first time in Opiliones. The phylogenetic implications of these compounds are briefly discussed in the scope of the present knowledge of Laniatores.

Keywords: Chemical ecology, defense, exocrine products, Arachnida, chemosystematics

A pair of large prosomal scent glands is an important synapomorphy of all Opiliones (Machado et al. 2007; Gnaspini & Hara 2007). These glands have traditionally been considered to play a. role in chemical defense (e.g., Martens 1978) and have been the subject of several investigations since the 1950's. Chemical data from scent gland secretions, even though strongly biased regarding certain groups, are meanwhile available for all four currently recognized suborders. So far, the chemical knowledge on the Cyphophthalmi, Eupnoi and Dyspnoi appears to be rather poor, relying on only three species of Cyphophthalmi (Raspotnig et al. 2005; Jones et al. 2009), about one dozen species of Eupnoi (e.g., Ekpa et al. 1985) and only one representative of Dyspnoi (Raspotnig et al. 2010). Also within the Eupnoi, data are strongly biased, mainly being available for North American Sclerosomatidae, *Leiobunum* spp. and one *Hadrobunus* species (Ekpa et al. 1985) and for one single species of Phalangiidae (Wiemer et al. 1978). In the Laniatores the situation appears to be similar: even though about 35 species have already been investigated, the major part of data originates from Gonyleptoidea such as cosmetids, gonyleptids, and manaosbiids (see Hara et al. 2005 and Gnaspini & Hara 2007 for references). In addition, chemical data are available for one species of Stygnommatidae (Duffield et al. 1981), one species of Travuniidae (Ekpa et al. 1984) and recently also for two species of Phalangodidae (Shear et al. 2010a). Chemical profiles of scent gland secretions in Opiliones are generally assumed to bear phylogenetically important information, as already emphazised by several authors (e.g., Duffield et al. 1981; Roach et al. 1980). In Gonyleptoidea, scent gland secretion bouquets are characterized by seemingly species-specific combinations of alkylated benzoquinones and phenols. Initial attempts to map these chemical products onto a preliminary gonyleptid phylogeny have already been published (Hara et al. 2005).

As outlined above, the use of scent gland profiles in opilionid systematics generally suffers from a hitherto rather poorly-founded chemical matrix and a patchy distribution of chemical data. Thus, in order to promote "chemosystematics" in Opiliones and to improve the chemical data base for Laniatores, we here report on the chemistry of the scent gland secretion of *Pachylus paessleri* Roewer 1913 (Gonyleptidae: Pachylinae). This study adds comparative knowledge to an assemblage of pachyline genera (*Pachylus* C.L. Koch 1839, *Acanthopachylus* Roewer 1913, *Pachyloidellus* Müller 1918) that are deemed to be close relatives (Acosta 2002; Acosta unpubl. data). The chemistry of scent gland products of *Acanthopachylus aculeatus* (Roewer 1913) has already been analyzed (Estable et al. 1955; Eisner et al. 2004) and that of *Pachyloidellus goliath* Acosta 1993 by Acosta et al. (1993).

We received four adult specimens (three females, one male) of *Pachylus paessleri* from Pedro Avaria (Avaria Import & Export, Bochum, Germany) in August 2008. This harvestman species occurs in central Chile, where it is quite common, though no capture data were available to us. One male and one female are deposited as voucher specimens in the Arachnological Collection, Cátedra de Diversidad Animal I, Faculty of Exact, Physical and Natural Sciences, National University of Córdoba, Argentina (CDA), identified as Pp-0-A and Pp-0-B. We kept the specimens alive for about one year in a terrarium that contained pieces of wood, bark, leaves, litter and soil, and we fed them dead insects (mainly house crickets *Acheta domesticus* and mealworm larvae *Tenebrio molitor*). For extraction of scent gland secretions, individuals were squeezed moderately by hand, which immediately resulted in the discharge of large yellowish droplets from the ozopores. We collected these droplets on small pieces of filter paper (~ 2 × 3mm) and extracted the secretion-loaded filter papers (along with non-loaded pieces of filter paper as a blank) in small amounts of hexane (150 µl). After extraction (for about 15 min), we used an aliquot of the extract (usually 1 µl) for injection into our GC-MS system. We performed the analyses on a Trace gas chromatograph GC2000 coupled to a Voyager mass spectrometer (ThermoQuest, Vienna, Austria). The GC-column (a ZB-5MS fused silica capillary column: 30 m × 0.25 mm i.d., 0.25 µm film thickness from Phenomenex, Germany) was directly connected to the ion source of the MS. The splitless Grob injector was kept at 260° C, and we used helium 5.6 (at a constant flow rate of 1.5ml/min) as a carrier gas. All data in the text refer to the following

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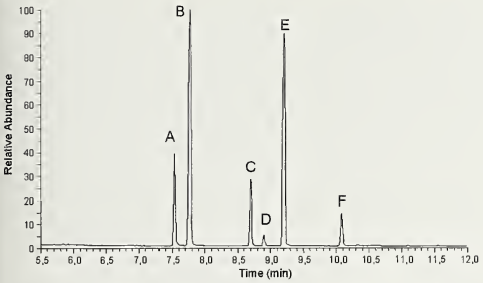


Figure 1.—Gas chromatographic profile of the scent gland secretion of a female of *Pachylus paessleri*. Each peak corresponds to a compound as follows: (A) 2,5-dimethyl-1,4-benzoquinone; (B) 2,3-dimethyl-1,4-benzoquinone; (C) 2-ethyl-3-methyl-1,4-benzoquinone; (D)* 2-ethyl-5-methyl-1,4-benzoquinone; (E)* 2,3,5-trimethyl-1,4-benzoquinone; (F)* 2,5-dimethyl-3-ethyl-1,4-benzoquinone. Compounds marked with asterisk* were tentatively identified on the basis of their mass spectra.

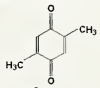
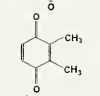
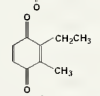
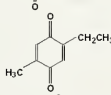
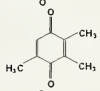
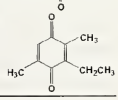
temperature program: Initial temperature 50° C for 1 min, followed by an increase of 10° C/min to 200° C, with 15° C/min to 300° C, and an isothermal hold for 5 min. The ion source of the mass spectrometer and the transfer line were kept at 170° C and 310° C, respectively. Electron impact (EI) spectra were recorded at 70eV. For reference, we used authentic 2,5-dimethyl-1,4-benzoquinone (Aldrich: Vienna, Austria). Quantification of compounds is based on the integration of peak areas in the chromatograms.

Secretions from both male and female *Pachylus paessleri* exhibited a consistent gas chromatographic pattern of six components in stable relative amounts (peaks A–F in Fig. 1). All components showed the mass spectral characteristics of alkylated 1,4-benzoquinones. In order to differentiate between the substitution patterns in di- or even tri-substituted benzoquinones, we followed the basic fragmentation patterns described for alkylated benzoquinones (e.g. Budzikiewicz et al. 1964; Machado et al. 2005): 1) loss of carbon monoxide; 2) loss of the most substituted acetylene; and 3) fission into two halves, with elimination of the most substituted neutral fragment. The latter mechanism provides diagnostic information on alkyl substitution in benzoquinones: in the case of asymmetrically substituted benzoquinones such as for 2,3-alkylation, fission into two halves leads to a prominent ion at m/z 54 (corresponding to the unsubstituted half of the molecule). By contrast, in case of alkyl substitution, other characteristic fragments are observed, corresponding to the fragment mentioned above, plus the mass of the respective alkyl-group (e.g., in symmetrically methylated benzoquinones, such as in 2,5-dimethyl-benzoquinone, a characteristic ion at m/z 68; i.e., 54 plus a CH_2-group, would be expected).

Compounds A and B, both showing a molecular ion at m/z 136 (Table 1), appeared to be isomeric dimethyl-benzoquinones or ethyl-benzoquinones, respectively. Compound A exhibited an EI-fragmentation pattern with a base ion at m/z 68 but no fragment at m/z 54, indicating a 2,5-dimethyl-1,4-benzoquinone. A comparison to an authentic sample showed full correspondence of both spectral comparison and gas chromatographic retention time. For compound B (having no fragment at m/z 68 in the spectrum) the structures of a 2-ethyl- or a 2,3-dimethyl-benzoquinone were possible. A comparison to the mass spectra of the authentic compounds (e.g., Machado et al. 2005) clearly supported the structure of a 2,3-dimethyl-1,4-benzoquinone.

All other components were tentatively identified on the basis of their mass spectra only (Table 1). Components C, D and E also appeared to be isomeric alkylated benzoquinones, all exhibiting molecular ions at m/z 150. This is consistent with structures of 1)

Table 1.—Mass spectrometric identification of secretion components in *Pachylus paessleri*.

Peak	Retention time (min)	Relative abundance (% peak area)	Fragmentation pattern m/z (relative intensity)	Identified structure	Formula
A	7.54	12	136 (79), 121 (3) 108 (37), 96 (24), 80 (21), 79 (46), 68 (100), 53 (8), 40 (36)	2,5-dimethyl-1,4-benzoquinone	
B	7.77	40	136 (100), 108 (69), 107 (76), 90 (16), 82 (69), 80 (32), 79 (85), 77 (18), 65 (11), 54 (87), 53 (45), 51 (27)	2,3-dimethyl-1,4-benzoquinone	
C	8.70	8	150 (100), 135 (11), 122 (36), 121 (19), 107 (93), 103 (7), 93 (10), 91 (10), 82 (37), 79 (61), 77 (29), 67 (19), 65 (16), 54 (41), 53 (28), 51 (14)	2-ethyl-3-methyl-1,4-benzoquinone	
D	8.90	1.5	150 (100), 135 (6), 122 (44), 121 (12), 107 (41), 103 (5), 96 (7), 93 (8), 91 (8), 82 (14), 79 (81), 77 (20), 68 (31), 67 (9), 54 (20), 53 (27), 51 (12), 40 (17)	2-ethyl-5-methyl-1,4-benzoquinone	
E	9.21	35	150 (100), 135 (3), 122 (75), 121 (42), 107 (93), 96 (30), 94 (23), 93 (26), 91 (17), 82 (17), 79 (91), 77 (36), 68 (93), 65 (10), 54 (53), 53 (50), 51 (30), 40 (36)	2,3,5-trimethyl-1,4-benzoquinone	
F	10.09	5	164 (95), 149 (15), 136 (28), 135 (14), 121 (100), 96 (9), 93 (39), 91 (22), 77 (20), 68 (25), 67 (22), 65 (12), 53 (18), 40 (17)	2,5-dimethyl-3-ethyl-1,4-benzoquinone	

ethyl-methyl-, 2) propyl-, and 3) trimethyl-benzoquinones, respectively. Comparisons of mass spectral data to spectra from the NIST-library did not lead to unequivocal results. Only compound C lacked a fragment at m/z 68, indicating alkyl-substitution at only one side of the ring; i.e., 2,3-substitution. This situation left only the possibility of 2-ethyl-3-methyl-1,4-benzoquinone open. In addition, the EI-mass spectrum of compound C completely matched the spectrum of 2-ethyl-3-methyl-1,4-benzoquinone as given in Machado et al. (2005). By contrast, both compounds D and E exhibited fragments at m/z 68 and were nearly indistinguishable by their EI mass spectra. Regarding the substitution patterns found in the already identified dimethyl-benzoquinones of *P. paessleri* (compounds A and B), the structures of 2-ethyl-5-methyl-1,4-benzoquinone and 2,3,5-trimethyl-1,4-benzoquinone appeared to be most likely. Since the latter compound is rather common and widely distributed in Gonyleptidae (see Gnaspini & Hara 2007), we tentatively propose the more abundant component E (about 35% of the secretion) to be 2,3,5-trimethyl-1,4-benzoquinone. Consequently, component D (a minor component) is proposed to be 2-ethyl-5-methyl-1,4-benzoquinone. The remaining component F had a molecular ion at m/z 164, indicating a further analogous benzoquinone, which contained an additional CH_2-moiety, thus a (C_4H_{12})-1,4-benzoquinone. The definitive substitution pattern was not further analysed, but - considering the components detected so far - it probably is a dimethyl-ethyl-1,4-benzoquinone. Along with a fragment ion at m/z 68 (indicating only one methyl-group on each side of the ring), the structure of 2,5-dimethyl-3-ethyl-1,4-benzoquinone is favored.

The two main components of *P. paessleri*, 2,3-dimethyl-1,4-benzoquinone (peak B) and 2,3,5-trimethyl-1,4-benzoquinone (peak E) together amounted for ¾ of the secretion. Both compounds are not only shared with its presumed relatives, *Pachyloidellus goliath* and *Acanthopachylus aculeatus*, but proved to be widespread in Gonyleptidae (Hara et al. 2005). They are present in at least four other separate lineages within this family (i.e., Goniosomatinae, Gonyleptinae, Sodreaninae and "Pachylinae 4" sensu Hara et al. 2005), though not detected in the clade containing the Progonyleptoidellinae and in some Goniosomatinae. The two compounds also appear to be distributed among other families of Gonyleptoidea investigated so far, both of them in the family Cosmetidae and 2,3-dimethyl-1,4-benzoquinone also in the Manaosbiidae (Eisner et al. 1971, 1977; Roach et al. 1980). The remaining methyl-benzoquinone of *P. paessleri* (2,5-dimethyl-1,4-benzoquinone = peak A: about 12% of the secretion) is also known from the closely related *Acanthopachylus aculeatus* (Estable et al. 1955; Eisner et al. 2004), and from *Paecilaema eutypa* (Chamberlin 1925), a cosmetid species (Eisner et al. 1977), but was not found in *P. goliath* nor elsewhere in the Gonyleptidae. On the other hand, ethyl-benzoquinones appear to be less widespread in laniatorean secretions. However, at least 2-ethyl-3-methyl-1,4-benzoquinone (component C of our study) has recently been identified in *Acutisoma longipes* Roewer 1913, a goniosomatine gonyleptid (Machado et al. 2005, there referred to genus *Goniosoma*). The latter compound, as well as 2-ethyl-5-methyl-1,4-benzoquinone (component D of *P. paessleri*), may also occur in several other gonyleptids of different subfamilies, but an exact identification of the specific isomers is so far missing in the literature (Hara et al. 2005). Thus, 2-ethyl-5-methyl-1,4-benzoquinone (component D) and 2,5-dimethyl-3-ethyl-1,4-benzoquinone (component F) may be new for laniatorean (and also opilionid) secretions. However, the dimethyl-ethyl-benzoquinone may already have been found in another pachyline species, *Pachyloidellus goliath*, but has been classified there as another isomer (as 2,3-dimethyl-3-ethyl-1,4-benzoquinone) (Acosta et al. 1993). Thus, opilionid benzoquinones appear to be rather derived characters in Laniatores, since they appear to be restricted to gonyleptoids. They have been found in the three families of Gonyleptoidea so far investigated (Gonyleptidae, Cosmetidae, Manaosbiidae), and they are especially predominant in subfamilies of the Gonyleptidae. Consequently, the two widespread methyl-benzoquinones (our peaks B and E) are probably symplesiomorphic on the taxonomic level of gonyleptoid families.

Regarding the plesiomorphic status of benzoquinones at the level of Pachylinae, not a single compound has been found to support the alleged relationship *Pachylus* + *Acanthopachylus* + *Pachyloidellus*. Nonetheless, in terms of similarity, the scent gland secretion profiles of *P. paessleri* and *A. aculeatus* look more similar to each other than to the secretion profile of *P. goliath*. This view is based on 1) 2,5-dimethyl-1,4-benzoquinone shared in secretions of *P. paessleri* and *A. aculeatus* while absent in other gonyleptids, including *P. goliath*, and 2) the lack of phenolic compounds (which represent a second chemical class in the secretion of *P. goliath*). These chemical affinities may be seen in accordance with the closer exomorphological similarities of *Pachylus* and *Acanthopachylus* (L.E. Acosta, pers. obs.). Also, the latter issue (i.e., presumed synapomorphic reduction of phenols) may provide a phylogenetic signal. Phenols may represent secretion components in laniatoreans that are phylogenetically older than benzoquinones. They are already present in the Phalangodoidea (rather basal Grassatores), as recently evidenced by the first investigation into the chemistry of the family Phalangodidae (Shear et al. 2010a), and 2-methyl-5-ethyl-phenol seems to represent an early compound (G. Raspotnig, unpubl. data). This and other phenols appear to be widespread in the secretions of Grassatores (e.g., Duffield et al. 1981), and are also still present in many Gonyleptoidea (e.g., some Cosmetidae, some Stygnopsidae, some Gonyleptidae), but presumably reduced in others (e.g., Eisner et al. 1977; Roach et al. 1980; Machado & Pomini 2008; Shear et al. 2010b). Disregarding the possibility of multiple convergent evolution, the presence of phenols in the secretion of *P. goliath* (Acosta *et al.* 1993) might thus be considered plesiomorphic. On the other hand, *P. paessleri* and *P. goliath* share ethyl-benzoquinones that might represent more derivative benzoquinone - characters of certain Gonyleptidae - this would relate *Pachylus* + *Pachyloidellus*, thus conflicting with the hypothesized clade *Pachylus* + *Acanthopachylus*. However, an ethyl-benzoquinone (homoplasy?) was also found in *Acutisoma longipes* (Machado et al. 2005), which is a representative of a clearly unrelated lineage, the Goniosomatinae.

This discussion shows how provisional our conclusions are at present. To develop the full potential of chemosystematics in the Opiliones, the generation of a reliable, comprehensive database is of uppermost importance. Not only more and more species (and lineages) should be incorporated into the chemical analyses, but compounds already reported might need confirmation and/or more analytical detail using modern techniques.

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SHORT COMMUNICATION

Trachyzelotes minutus, a new zelotine ground spider (Araneae: Gnaphosidae: Zavattaricinae) species from southern Portugal

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Abstract. A new *Trachyzelotes* spider species, *Trachyzelotes minutus* n. sp. is described. The new species likely belongs to the "*barbatus* group", based on the rounded embolus base and terminal apophysis, as well as the anterolaterally expanded copulatory ducts. *Trachyzelotes minutus* may be a sister species of *T. fuscipes*, given the similarities of the embolus and terminal apophysis.

Keywords: Iberian Peninsula, Mediterranean, taxonomy

The genus *Trachyzelotes* Lohmander 1944 is a well-known genus of the gnaphosid subfamily Zavattaricinae Caporiacco 1941 (Platnick 1992). It was initially designated as a subgroup of the large genus *Zelotes* Gistel 1848 by Lohmander and was elevated to genus status by Platnick & Murphy (1984), who revised the genus as well. Additional species were described later through isolated descriptions by several other authors (Xu 1991; Tuneva & Esyunin 2002; Ponomarev & Tsvetkov 2006; Levy 2009) and two species, *T. cumensis* (Ponomarev 1979) and *T. glossus* (Strand 1915), were transferred from *Zelotes* Gistel 1848 (Ponomarev & Tsvetkov 2004; Levy 1998, respectively).

Spiders of this genus can be diagnosed by a cluster of dense stiff setae on the anteromedian surface of the chelicerae. Platnick & Murphy (1984) also distinguished three groups of species according to genitalic morphology: a monospecific group with the type species, *T. pedestris* (C.L. Koch 1837), in which males show an elongated terminal apophysis and females display massive and fused anterior epigynal ducts; the *lyonneti* group, in which males exhibit obliquely oriented terminal apophyses and embolar bases and females show a semicircular anterior epigynal margin; finally, the *barbatus* group, in which males carry rounded terminal apophyses and embolar bases and females have anterolaterally expanded epigynal ducts.

Trachyzelotes species, like typical gnaphosid ground spiders, are mostly active at night, wandering at ground level and are likely generalist predators. The genus is present throughout both Old and New World; however, it does show a greater diversity of species in the Old World, with only four species cited to the New World (*T. barbatus* (L. Koch 1866), *T. jaxartensis* (Kroneberg 1875), *T. kulczynskii* (Bösenberg 1902) and *T. lyonneti* (Audouin 1826)), all of which are presumed native to Europe or to the Mediterranean (Platnick & Murphy 1984). In general, of the total 18 species currently described, 12 are Mediterranean. Possibly some older descriptions of *Zelotes* species outside the Mediterranean may actually be *Trachyzelotes*. In Portugal, six species are currently known, and all but one are members of the *barbatus* group: *T. fuscipes* (L. Koch 1866), *T. holosericeus* (Simon 1878), *T. pedestris* (C.L. Koch 1837), *T. bardiae* (Caporiacco 1928), *T. mutabilis* (Simon 1878), and *T. barbatus* (L. Koch 1837), with the most common species being *T. fuscipes* (see Cardoso 2010).

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TAXONOMY

Trachyzelotes Lohmander 1944

Type species.—*T. pedestris* (C.L. Koch 1837)

Trachyzelotes minutus Crespo, new species
(Figs. 1–9)

Material examined.—PORTUGAL: *Évora*: Holotype male, Corval, Reguengos de Monsaraz County, coordinates 29SPC26 (UTM, 10 × 10 km squares). Female paratypes (two specimens, one of which has the epigynum removed; the latter was accidentally lost) from Montoito, Redondo County, Évora District, coordinates 29SPC17. Sara Mendes collected all specimens in pitfall traps on 2–16 June 2008 at two sites, both cork oak (*Quercus ilex* L.) woodland with scattered shrubs. We found a considerable number of specimens of rockrose *Cistus ladanifer* L. in Corval.

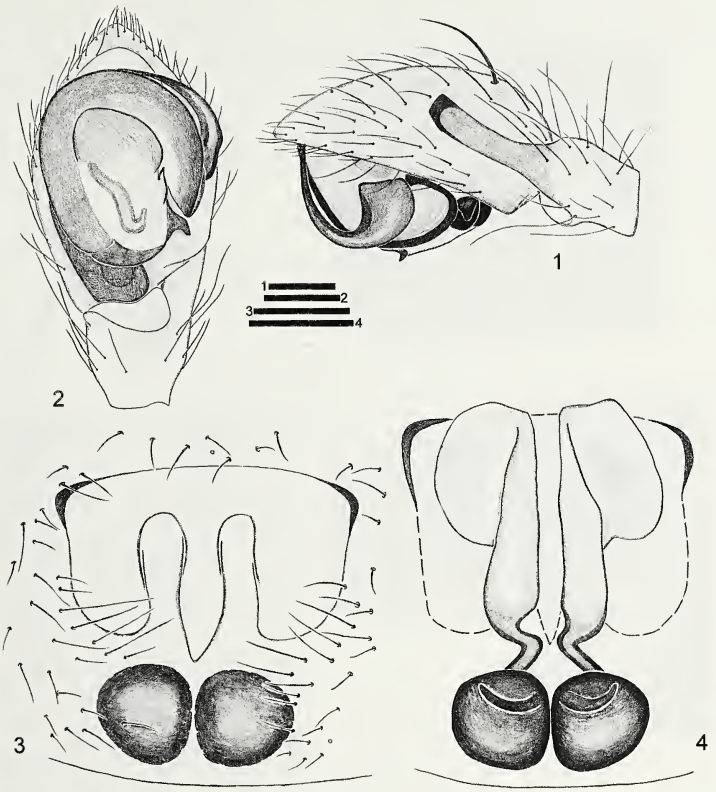
Depository.—All three specimens are deposited in the Zoological Museum of Copenhagen. The male holotype is catalogued as ZMUC00012693 and the female paratypes are catalogued as ZMUC00012694.

Etymology.—The name refers to the species' small size, making it the smallest known species of *Trachyzelotes*.

Other material.—*T. bardiae*: Paúl de Arzila Natural Reserve, 1 male, 1 female, 31 May 2006, hand collected; 1 male, 28 May 2008, pitfall trap, collected by the author. *T. fuscipes*: Paúl de Arzila Natural Reserve, 1 female, 2 July 2006, hand collected; 1 male, 28 May 2008, pitfall trap, collected by the author and colleagues. *T. holosericeus*: Paúl de Arzila Natural Reserve, 1 male, 1 female, 31 May 2006, pitfall trap, collected by the author.

Diagnosis.—This species can be distinguished from all other *Trachyzelotes* by its small size, by the male palp that shows a basally wide embolus curving 180° retrolaterally and gradually narrowing toward the tip, and also by its obliquely elongated tibial apophysis that carries a blunt tip. Females can be identified by the touching spermathecae and the very short spermathecal ducts that converge up to two- thirds of their total length and diverge in the final third.

Description.—Total length: 2.38 (male), 2.36–2.97 (females); Prosoma: 0.95 long, 0.72 wide (male), 0.98–1.11 long, 0.76–0.88 wide (females). Eyes: AME 0.02 (male), 0.03 (females); ALE 0.03 (male), 0.05 (females); PLE 0.04; PME 0.04 (male), 0.05 (females); PME–PME 0.03; PME–PLE 0.02 (male), 0.03 (females); PLE–ALE 0.01; AME–AME 0.02 (male), 0.03 (female); AME–ALE 0.01 (male), touching in females; AME–PME 0.04; AME dark, rounded, others light, oval; PER slightly procurved; AER straight. Carapace oval, truncated anteriorly and posteriorly, with widest point at

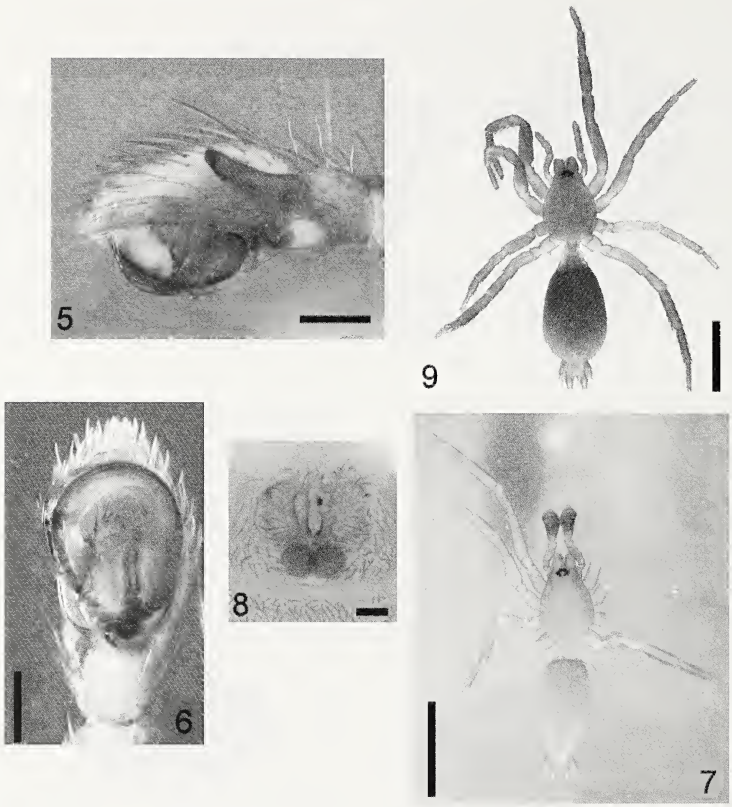


Figures 1–4.—Drawings of adult *Trachyzelotes minutus*. 1. Retrolateral aspect of left pedipalp of male from Corval; 2. Ventral aspect of left pedipalp of male from Corval; 3. Ventral aspect of epigynum of female from Montoito; 4. Dorsal aspect of the vulvar structure of female from Montoito. Scale bars = 0.1 mm.

superior limit of coxa III; yellow-grayish with some ill-defined gray stripes radiating towards legs, with sparse simple hairs. Clypeal height at AME two times their diameter; at ALE about two-thirds their diameter. Sternum oval, anteriorly truncated, with no sclerotized extensions to coxae, with hairs present uniformly around margin, sparsely in middle section. Labium 0.16 wide basally, 0.13 long (male), 0.14–0.19 wide basally, 0.15–0.18 long (females), with anterior margin convex, each maxilla converging up to one-third of labium width, in one female less convergent. Chelicerae: retromargin without teeth, promargin with 3 small teeth. Cluster of stiff setae present but not very dense. Opisthosoma: Gray, with simple hairs throughout most of its extension, but for anterodorsal region, which presents serrated long hairs, male presents a rudimentary yellowish triangular scutum; both sexes present two parallel lines of intermittent small regions with no hairs in middle dorsal opisthosoma. Legs: Yellow-grayish, with terminal segments only very slightly darker; metatarsal comb present; pilosity irregularly scattered, with hair patterns visible on ventrolateral surface of femora as continuous rows of hairs that may or may not occupy full length of femur, as rings of hairs on distal margin and ventrolateral surface of each segment other than femora; tarsal claws with 3 teeth on ventral surface; see leg sizes in Table 1 and spination in Table 2. Male palp (Figs. 1, 2, 5, 6): pedipalp with obliquely elongated tibial apophysis with darkened blunt tip. Embolus basally wide, narrowing toward tip while curving 180° retrolaterally, embolus base rounded. Terminal apophysis rounded, below with small spur directed anteriorly and outward, median apophysis hook-shaped, distally truncated ventrally. Epigynum (Figs. 3, 8): Epigynal ridge subrectangular, wider than long, with two long prongs emerging from posterior margin, directed anteriorly, reaching about two-thirds of total ridge length. Vulva (Fig. 4): Spermathecae roughly quadrangular, small, touching; spermathecal ducts very small, converging up to two-thirds of their length, diverging in last third into copulatory ducts that are tubuliform, elongated at their posterior end, gradually narrowing to constriction that expands anterolaterally into irregular ovoid shape.

DISCUSSION

This species is clearly a member of the *barbatus* group, given the rounded embolus base and terminal apophysis, as well as the



Figures 5–9.—Photographs of adult *Trachyzelotes minutus*. 5–7. Male from Corval: 5. Retrolateral aspect of left pedipalp; 6. Ventral aspect of right pedipalp; 7. Habitus. 8, 9. Female from Montoito: 8. Ventral aspect of epigynum; 9. Habitus. Scale bars = 0.1 mm (5, 6, 8); 1 mm (7, 9).

anterolaterally expanded copulatory ducts. Within the group, it seems that the species might be closest to *T. fuscipes* given the similarities of the embolus base, terminal apophysis and median apophysis. This close relationship to *T. fuscipes* is mirrored in the females as well with the touching spermathecae and the two prongs in the posterior margin of the epigynal ridge. However, characters like the small size, the spermathecal and copulatory ducts in the female, and the embolus or the tibial apophysis in the male clearly separate these two species.

Table 1.—Size of pedipalps and legs in *Trachyzelotes minutus*. For each measurement, value for holotype male is shown above those for two paratype females.

	Coxa	Femur	Patella	Tibia	Metatarsus	Tarsus
Pedipalp	0.12	0.34	0.13	0.1	-	0.3
	0.14	0.33	0.12, 0.14	0.11, 0.13	-	0.20, 0.28
Leg I	0.35	0.67	0.43	0.5	0.38	0.42
	0.33	0.71, 0.76	0.43	0.50, 0.52	0.38	0.41, 0.42
Leg II	0.28	0.57	0.38	0.41	0.35	0.38
	0.24, 0.27	0.59, 0.64	0.33, 0.41	0.38	0.35, 0.36	0.35, 0.38
Leg III	0.2	0.48	0.23	0.3	0.33	0.3
	0.21, 0.24	0.48, 0.50	0.30, 0.35	0.31, 0.41	0.30, 0.40	0.34, 0.38
Leg IV	0.33	0.67	0.39	0.57	0.56	0.39
	0.33, 0.37	0.68, 0.76	0.31, 0.41	0.52	0.50, 0.52	0.37, 0.45

Table 2.—Leg spination of *Trachyzelotes minutus*. For each measurement, holotype male is shown on top of the two paratype females, and the spine formula should be interpreted as (dorsal–prolateral–retrolateral–ventral); a 'p' stands for pair and parentheses indicate a variable spine formation. A sequence is indicated by a 'x+y' from proximal to distal length. Segments that do not bear any spine are not shown.

	Femur	Tibia	Metatarsus
Leg I	1-0-0-0	-	-
	1-0-0-0	-	-
Leg II	1-0-0-0	-	-
	1-0-0-0	-	0-0-0-1(0)
Leg III	2-1-0-0	0-2-1-1+1p	0-1-2-0
	2-1-0(1)-0	0-2(3)-2-1+1p(2p)	0-1(4)-2(3)-0
Leg IV	2-0-1-0	0-3-4-1+2p	0-4-4-0
	2-0-1-0	0-3-4(3)-1+2p(3p)	0-4(7)-4-0

Four species were described after the revision by Platnick & Murphy (1984), *T. baiyuensis* Xu 1991, *T. chybyndensis* Tuneva & Esyunin 2002, *T. cumensis* (Ponomarev 1979) and *T. glossus* (Strand 1915). Literature containing the descriptions of these species was obtained to compare each species with the hereby described material, and the differences in the morphology of the genitalia are clear.

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We thank Pedro Cardoso for the loan of his microscope and for all the help on the illustrations and photographs, to Nikolaj Scharff for his willingness to hold the material in the ZMUC collection, to Antonio Melic for comments on the existence of *T. minutus* in material previously collected, to A. Ponomarev for access to literature and photographs of *T. cumensis* and *T. manytchensis*, to Gershom Levy for his paper on Israeli zelotines in which he illustrates *T. glossus*, to Rudy Jocqué for his useful comments on earlier versions of the illustrations provided, and to Alain Reygel for hints on illustrating with pencil.

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SHORT COMMUNICATION

Notes on two coelotine spiders from Japan (Araneae: Agelenidae)

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Abstract. Two spider species of the subfamily Coelotinae from Japan, *Coelotes decolor* Nishikawa 1973 and *Hypocoelotes tumidivulva* (Nishikawa 1980), are revised. We focus particularly on the female vulva structures, which are illustrated and described for the first time. Both species have unique genitalic structures compared with other coelotines. The female *Coelotes decolor* is similar to *C. akakinaensis* Shimojana 2000 and *C. iheyaensis* Shimojana 2000 in having long spermathecal stalks, but no species have been found to be similar to *Hypocoelotes tumidivulva*.

Keywords: *Coelotes*, *Hypocoelotes*, morphology, vulva

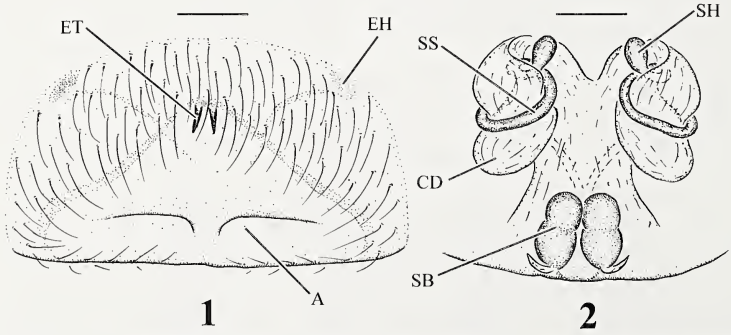
Coelotine spiders have similar somatic appearances but rather diversified genitalic structures. In most cases, the ventral view of the epigynum will provide enough information to identify the female, but the dorsal, or inside, view of epigynum, which reveals the vulva tubes, could not only help researchers identify the species, but also could serve as an important estimation of their phylogenetic relationships within the subfamily Coelotinae F.O. Pickard-Cambridge 1893. The structures observed in dorsal view of the epigynum in coelotines include the fertilization ducts, copulatory ducts, and spermathecae. The fertilization ducts are consistently short and slender, arising from proximal spermathecae, but copulatory ducts and spermathecae vary among coelotine species.

Two ceolotines featured in publications by Nishikawa separately in 1973 and 1980 from Japan showed distinctly different epigyna in ventral view: *Coelotes decolor* Nishikawa 1973 and *Coelotes tumidivulva* Nishikawa 1980. Unfortunately, the vulva structures were neither described nor illustrated in either species. Since then several studies have been made (Nishikawa 1974, 1987, 2009; Shinkai 1978; Yaginuma 1986; Chikuni 1989; Okumura et al. 2009), and a new genus, *Hypocoelotes* Nishikawa 2009, has been proposed to accommodate *Coelotes tumidivulva*, but regrettably no vulva structures were explored in these studies.

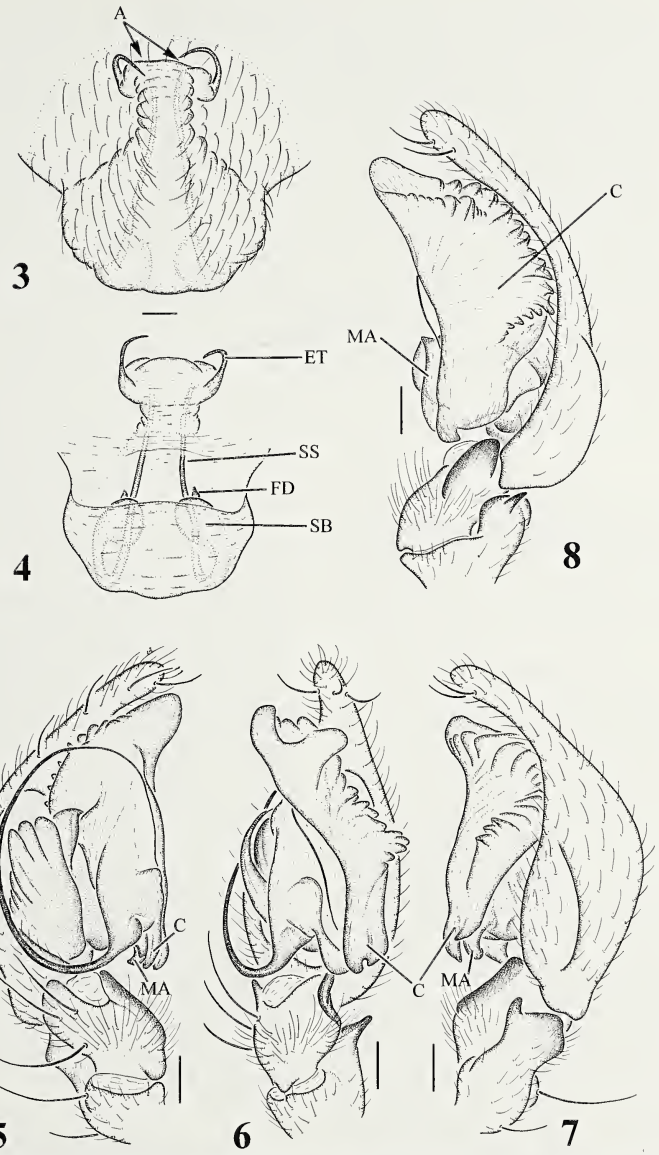
In this paper, we explored the details of the vulva of both species and found that they have distinctly different structures. In addition to the epigynum, the male palp of *Hypocoelotes tumidivulvus* (Nishikawa 1980) was also re-illustrated to reveal the details, which are missing in previous studies.

Abbreviations used in the text are: *Eyes*: AME–anterior median eyes; ALE–anterior lateral eyes; PLE–posterior lateral eyes; PME–posterior median eyes. *Epigynum*: A–atrium; CD–copulatory duct; EH–epigynal hood; ET–epigynal tooth; FD–fertilization duct; S–spermathecae; SB–spermathecal base; SS–spermathecal stalk; SH–spermathecal head. *Palp*: C–conductor; MA–median apophysis; RTA–retrolateral tibial apophysis.

The material examined in the current paper is deposited in the National Museum of Nature and Science (former National Science Museum), Tokyo (NSMT). Scale lines = 0.2 mm. Terminology used in the text and figures follows Wang (2002). The distribution map was created using ArcView GIS software, and distribution data are collected from Nishikawa (1973, 1987). In this study we follow Miller



Figures 1, 2.—*Coelotes decolor* Nishikawa 1973, female from Goto Islands, Japan, epigynum. 1. Ventral view; 2. Dorsal view.



Figures 3–8.—*Hypocoelotes tumidivulva* (Nishikawa 1980), female from Gifu, Japan. 3. Epigynum, ventral view; 4. Epigynum, dorsal view; 5. Palp, prolateral view; 6. Palp, ventral view; 7–8. Palp, retrolateral view.

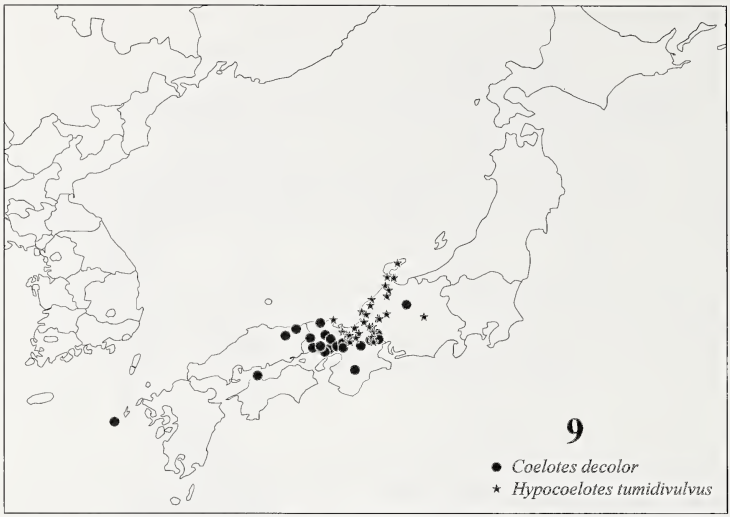


Figure 9. Map of Japan, showing the distribution records of *Coelotes decolor* Nishikawa 1973 (dark circle) and *Hypocoelotes tumidivulva* (Nishikawa 1980) (dark star). Data from Nishikawa (1973, 1987).

et al. (2010) and list Coelotinae as a subfamily of the family Agelenidae, rather than Amaurobiidae.

TAXONOMY

Agelenidae C.L. Koch 1837
Coelotinae F.O. Pickard-Cambridge 1893

Coelotes Blackwall 1841
Coelotes decolor Nishikawa 1973
(Figs. 1, 2, 9)

Coelotes decolor Nishikawa 1973:75, figs. 1–5 (female holotype and male paratype from Hyogo Prefecture, Japan, in the Arachnological Society of Japan, c/o Otemon Gakuin University, Ibaraki, Osaka, not examined); Nishikawa 1974:178, figs. 27, 28; Nishikawa 1976:1056, fig. 11; Shinkai 1978:95, figs. 33, 34; Yaginuma 1986:151, fig. 82.9; Chikuni 1989:102, fig. 17; Okumura et al. 2009:187, figs. 183–187.

Material examined.—JAPAN: *Nagasaki Prefecture*: Gotō Islands, Fukue-jima, Tomie-cho, Takego, No-ana Cave, October 4, 1970, 1♀ S.-I. Uéno leg. (NSMT-Ar 91).

Diagnosis.—The female is similar to *C. akakinaensis* Shimojana 2000 and *C. iheyaensis* Shimojana 2000 in having tiny, anteriorly arising, closely set epigynal teeth and long, coiled, anteriorly extending spermathecal stalks, but can be distinguished by the small, posteriorly situated atrium (Figs. 1, 2). The male can be recognized by the broad, short conductor and long, broad embolus (Nishikawa 1973:figs. 3–5; Okumura et al. 2009:figs. 186, 187).

Description.—Described by Nishikawa (1973), but female vulva was neither illustrated nor described.

Female: Medium to large-sized coelotine, total length 8.00–11.00. AME smallest, about half the size of ALE, posterior eyes subequal in size, ¾ size of ALE; anterior eyes equally separated by slightly less than AME diameter; PME separated from each other by about their diameter, from PLE by about 1.2 times PME diameter. Chelicera with 3 promarginal and 2 retromarginal teeth. Labium slightly longer than wide. Epigynal teeth tiny, arising anteriorly at level of epigynal hoods, closely set, distinctly separated from atrium by 2–3 times atrial length; atrium wider than long, situated posteriorly close to epigastric furrow, with distinct posteriorly protruding anterior margin, lateral margins indistinct; copulatory ducts large, originating posteriorly, closely set, extending medially and anteriorly, then diverging and extending laterally and posteriorly, forming two large sacs around which the spermathecal stalks coil; spermathecae with bases broad, closely set, slightly extending anteriorly; spermathecal stalks long, slender, arising close together from anterior part of spermathecal bases, diverging and coiling around anterior part of copulatory ducts; spermathecal heads large, arising anteriorly (Figs. 1, 2).

Male: Medium sized coelotine, total length 8.00–9.50. Chelicera with 3 promarginal and 2 retromarginal teeth. Palp with a small patellar apophysis; RTA more than half of tibial length, with slightly protruding distal end; lateral tibial apophysis, which is a small apophysis arising from dorsal side of RTA in most coelotines (Wang 2003:fig. 2D), present; cymbial furrow less than half of cymbial length; cymbium with 5 distinct trichobothria retrolaterally close to distal cymbial furrow; conductor broad, short, deeply grooved; median apophysis spoon-shaped, not elongate along anterior edge; embolus long, broad, originating between prolateral and proximal, not coiled beyond distal part of bulb (Nishikawa 1973:figs. 3–5; Okumura *et al.* 2009:figs. 186, 187).

Distribution.—Japan (Fig. 9).

Hypocoelotes Nishikawa 2009
Hypocoelotes tumidivulva (Nishikawa 1980)
(Figs. 3–9)

Coelotes tumidivulva Nishikawa 1980:39, figs. 1–12 (female holotype and male allotype from Gifu Prefecture, Japan, in NSMT, examined); Yaginuma 1986:151, fig. 82.11; Nishikawa 1987:443, fig. 106; Chikuni 1989:102, fig. 18.
Coelotes tumidivulvus Platnick 2010.

Hypocoelotes tumidivulva Okumura et al. 2009:178, figs. 46–52 (note: the name *tumidivulva* is a noun and need not agree in gender with the generic name).

Material examined.—JAPAN: *Gifu Prefecture*: east slope of the Nukumi-toge pass, 950 m, north of Mt. Nogo-Hakusan, October 4, 1980, 1♀ (holotype, NSMT-Ar. 420), 1♂ (allotype, NSMT-Ar. 421), Y. Nishikawa.

Diagnosis.—This species can be easily distinguished from other coelotines by the large, posteriorly protruding epigynal plate and slender, anteriorly originating, posteriorly extending spermathecal stalks in the female, and by the broad patellar apophysis, absence of lateral tibial apophysis, absence of conductor dorsal apophysis, broad, posteriorly extending, strongly wrinkled conductor in the male (Figs. 3–8).

Description.—Described by Nishikawa (1980), but female vulva was neither illustrated nor described.

Female: Medium-sized coelotine, total length 6.60 (holotype). AME smallest, less than half the size of ALE, ALE largest; posterior eyes subequal in size, with PLE slightly larger; AME separated from each other by about their diameter, from ALE by slightly less than AME diameter; posterior eyes equally separated by about their diameter. Chelicera with 3 promarginal and 2 retromarginal teeth. Labium length subequal to width. Epigynum with a large, anteriorly narrow and posteriorly broad, distinctly protruding plate; epigynal teeth short, slender, arising anteriorly, moderately separated; atrium reduced to a slit, situated anteriorly close to epigynal teeth; copulatory ducts small, close to epigynal teeth; spermathecae with long, slender stalks arising anteriorly and extending posteriorly to posterior protrusion of epigynal plate, slightly curved back anteriorly to small, round spermathecal bases; spermathecal bases separated by slightly less than their width; spermathecal heads invisible from dorsal view; fertilization ducts small, arising anteriorly on spermathecal bases (Figs. 3, 4).

Male: Medium-sized coelotine, total length 6.10 (allotype). Palp with patellar apophysis as broad as patella, with a small distal tooth; RTA slightly more than half of tibial length, with blunt distal end; lateral tibial apophysis absent; cymbium furrow less than half of cymbial length; conductor broad, long, extending posteriorly to base of embolus, slightly notched and toothed distally, distinctly wrinkled dorsally, without dorsal apophysis and basal lamella; median apophysis small, spoon-shaped, covered by conductor in ventral view; embolus filiform, long, with small base, proximal in origin, not coiled beyond distal part of bulb (Figs. 5–8).

Distribution.—Japan (Fig. 9).

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SHORT COMMUNICATION

Mesothelae have venom glands

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Abstract. Although venom glands were described for the Mesothelae many years ago (Bristowe & Millot 1933), a more recent monograph (Haupt 2003) denied the existence of such glands in the Mesothelae. Our morphological studies of nine different species of *Liphistius* demonstrated the presence of venom gland openings on the cheliceral fangs in all of these species. Also, we observed a small venom gland in the anterior portion of the cheliceral basal segment. The possibility that venom glands may be lacking in adult males is discussed. The presence of venom glands in the Mesothelae indicates that this is a plesiomorphic character of all Araneae.

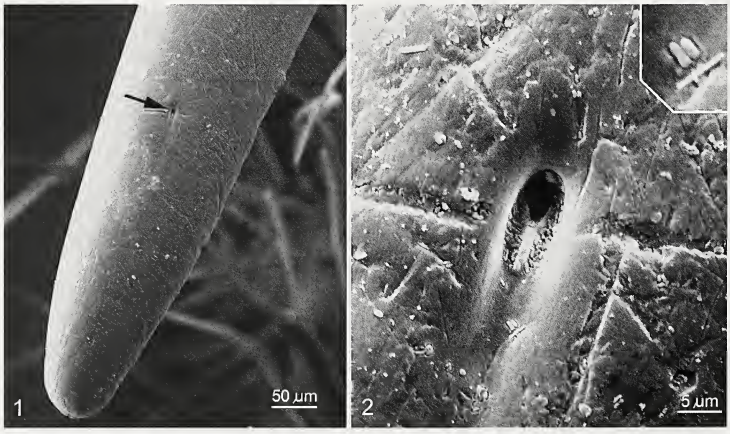
Keywords: *Liphistius*, venom glands

A venomous bite is a typical feature of most spiders. Only members of the family Uloboridae lack venom glands (Millot 1931), but most likely they lost them secondarily. Recently it was claimed that the ancient Mesothelae (Liphistiidae) also lack venom glands (Haupt 2003). This claim contradicts an earlier study in which small venom glands were described for *Liphistius desultor* (Bristowe & Millot 1933). The aim of the present study was to examine a number of species of *Liphistius* to check whether venom glands are present or not. Our first step was to inspect the cheliceral fangs with a scanning electron microscope to see if they have venom gland openings, as is generally the case in spiders. In a second step, we dissected some chelicerae under a binocular microscope in order to find the venom gland itself.

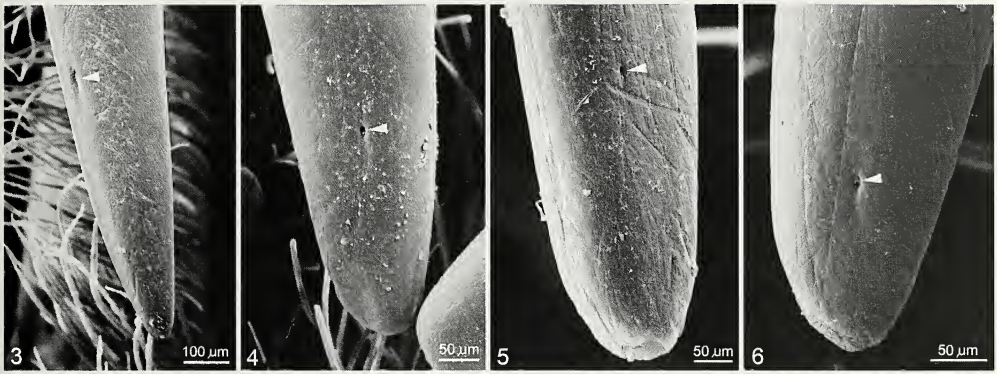
Most specimens were provided by Dr. Peter Schwendinger of the Muséum d'histoire naturelle in Geneva, Switzerland. Specimens fixed in alcohol or exuviae of the following nine species were at our disposal: *L. bicoloripes* Ono, 1988, *L. bristowei* Platnick & Sedgwick, 1984, *L. dangrek* Schwendinger, 1996, *L. desultor* Schiødte, 1849, *L. endau* Sedgwick & Platnick, 1987, *L. malayanus* Abraham, 1923, *L. niphanae* Ono, 1988, *L. sunatranus* Thorell, 1890, und *L. yanasakii* Ono, 1988. Isolated chelicerae were dehydrated in alcohol and acetone and then transferred to HMDS (Hexamethyldisilazane; Nation 1983) for 10 min to avoid shrinkage, before air drying on filter paper. After being sputtered with gold, we examined them from different angles in a Zeiss DSM 950 scanning electron microscope (SEM) at 15 kV.

We performed dissections of chelicerae placed in alcohol using watch maker forceps and micro-scalpels (razor blade fragments). Isolated venom glands were studied under various illuminations with a Leitz light microscope; best results were obtained under polarized light.

Since venom glands in orthognath spiders are relatively small and thus difficult to find, it seemed easier to begin by simply looking for any pore openings of possible glands near the tip of the cheliceral fangs. In most labidognath spiders, these openings are rather large



Figures 1, 2.—Cheliceral fang in *Liphistius bristowei*. 1. Ventral view; the opening of the venom gland (arrow) is barely visible and lies far away from the tip of the fang. 2. Higher magnification of the pore shows a slipper-shaped opening. Note the tiny rods inside the pore which represent bacteria (*Inset*).



Figures 3–6.—Ventral view of cheliceral fangs in different *Liphistius* species; the arrowhead points to the opening of the venom gland. 3. *L. desultor*; 4. *L. niphanae*; 5. *L. yamasakii*; 6. *L. endau*.

and are situated on the backside of the cheliceral fangs, close to the tip. In orthognath spiders (theraphosids), they lie in a different location, namely at the convex side of the cheliceral fang and can only be seen if viewed directly from the ventral side. We found that this is also the case in the Mesothelae (Foelix & Erb 2010). Two other factors make these openings difficult to detect: (1) they lie relatively far away from the tip of the cheliceral fang, usually 300–400 µm (Fig. 1), and (2) they are very small, measuring only 5–10 µm in diameter (Fig. 2). However, after having found such a pore opening on one chelicera, we always found it possible to identify the corresponding pore (same location, same size) on the other chelicera. This was true for all the species examined in this study (Figs. 3–6). Only in a few cases were we unable to detect these openings. Whether this is really "evidence for absence" is hard to say, but we offer a possible explanation in the Discussion.

Finding the venom glands in *Liphistius* also presents a challenge. The entire basal segment of a chelicera is packed with muscle tissue and in fresh material we were unable to locate any gland, despite knowing where to expect to find it. We were more successful, however, when using alcohol-fixed material. There the muscle tissue forms solid bundles of individual muscle fibers which can be plucked out in a stepwise fashion with watch maker forceps. Only when almost all muscle fibers have been removed, does the venom gland gradually appear, right behind the insertion of the cheliceral fang into the basal segment (Fig. 7). The body of the gland is about 1.5 mm long and 0.5 mm wide and is surrounded by a "spiraling" muscle layer. (Fig. 8). Under polarized light, a distinct herring-bone pattern becomes visible, caused by parallel muscle fibers arising obliquely from a longitudinal line ("backbone"). Actually, the muscle fibers do not really spiral around the body of the gland but several rectangular muscle cells are arranged serially and form a kind of belt. At higher magnification these muscle fibers show a marked cross-striation (Fig. 9) which indicates that they can contract voluntarily. The gland itself lies underneath that muscle layer but no details could be seen in our whole mount preparations. We found the venom gland in the chelicerae of a female (*L. bicoloripes*) but not in the single male specimen (*L. dangrek*) that we had available for dissection, so we cannot be sure whether this absence is typical for all male *Liphistius* spiders.

Our study indicates that Mesothelae (*Liphistius* species) do possess venom glands since we could detect venom gland openings on the cheliceral fangs in nine species. We also found the venom gland itself, at least in the female. This is in accord with an early publication by Bristowe & Millot (1933), in which Millot described a small venom gland in *L. desultor*, and also included a detailed sketch of its location and its microscopical structure. Millot's main conclusion was that the venom gland in *Liphistius* is morphologically identical to the venom gland in theraphosids. In contrast, in his monograph on Mesothelae, Haupt (2003) stated that "Mesothelae lack such venom glands," and "there is no pit on the fang indicating the opening of the gland." The latter claim can now be refuted, as our SEM pictures definitively show the presence of such a pore in all the nine species examined (Figs. 3–6). The fact that Haupt (2003) did not see any pore openings in the light microscope can perhaps be explained by the thick cuticle of the cheliceral fang and the tiny size of these pores (5–10 µm). It is more difficult to understand why his SEM pictures do not show any pore openings either, although the orientation of the cheliceral fang seems correct (ventral side up). However, the magnification he used in the SEM was rather low and the small pores could be clogged. There is another possible explanation: perhaps he was looking only at adult male chelicerae, which may lack such pores. Since *Liphistius* males are very short-lived and hardly capture any prey as adults (Schwendinger, pers. comm.), it could well be that they have reduced or lost their venom glands with their final molt. It is known from other spiders that the adult males may lose certain characters with their last molt, [e.g., male cribellate spiders lose their cribellum and calamistrum, and male orb weavers lose their triad spigots that normally produce the sticky capture thread (Foelix 2011)]. What needs to be done in future studies is to focus on adult male *Liphistius* and check specifically for the presence or absence of venom glands.

Clearly, Mesothelae have venom glands, at least in the female and juveniles. Their general presence in *Liphistius* implies that this is an ancient (plesiomorphic) feature and not an apomorphic character of the Opisthothelae, as suggested by Haupt (2003).

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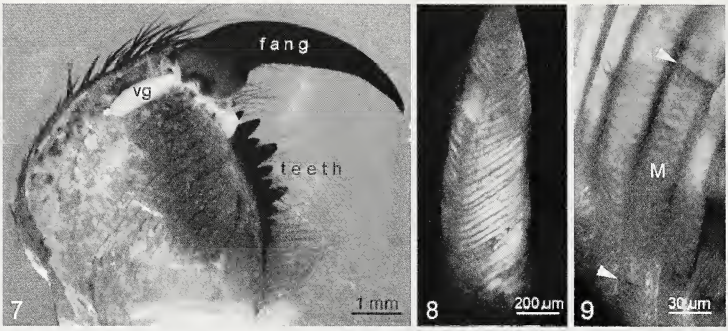
Our thanks go to Dr. Peter Schwendinger (Muséum d'histoire naturelle, Geneva) for providing us with most of the *Liphistius* material and for many valuable discussions, and also to Chris Sainsbury for sending us a *male L. dangrek*. Jan de Vries, Dieter Ertinger, and Peter Wagner generously helped with technical problems related to electron microscopy. For critical reading of the manuscript we are indebted to Jerome Rovner.



Figures 7–9.—Venom glands in *Liphistius bicoloripes*. 7. Dissection of a chelicera showing the location of the venom gland (vg) behind the articulation of the fang; all muscle tissue has been removed from the basal segment of the chelicera. 8. Isolated venom gland under the microscope using polarized light; muscle fibers surrounding the gland are arranged in a herringbone pattern. 9. Higher magnification view of the muscle layer reveals the cell borders (arrowheads) of adjacent muscle cells (M) and the distinct cross-striation of the cytoplasm.

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SHORT COMMUNICATION

Scopulate hairs in male *Liphistius* spiders: probable contact chemoreceptors

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Abstract. Adult male *Liphistius* have dense hair pads on the ventral side of their tarsi. At first glance they appear like the adhesive scopulae, which are well known from mygalomorph spiders. However, a fine structural analysis of these scopulate hairs shows that they lack the brush-like structure with tiny "endfeet" that is typical for such adhesive hairs. Instead, the smooth hair shaft exhibits a small pore ventrally, about 8–10 µm from the blunt tip. A thin cuticular canal extends from that pore through the middle of the hair shaft and terminates about 30 µm above the hair base. Transmission electron mieroscopy reveals that this central canal contains about 16 delicate dendrites. The morphology of these scopulate hairs thus corresponds closely to contact chemoreceptors known from other spiders. Since these scopulate hairs occur only in adult males, they are likely involved in the perception of female pheromones.

Keywords: Morphology, scopulae, Mesothelae

Many wandering spiders possess dense hair pads (scopulae) on the ventral side of their tarsi. Such scopula hairs have a brush-like appearance, and they serve to enhance adhesion to the substrate (Homann 1957; Hill 1977; Foelix 1985a; Kesel et al. 2003). With the aid of the distal-most hair pad (claw tuft), spiders can move sure-footedly on smooth, vertical surfaces. The more extensive hair pads on the proximal tarsus (and often metatarsus) are not involved in walking, but enable a spider to achieve a firm grip on its prey (Rovner 1978; Foelix et al. 1984). The ancient mesothele spiders in the genus *Liphistius* also exhibit tarsal "scopulae," but only in the adult males. A eloser inspection with the scanning electron microscope showed that the structure of these scopulate hairs is quite different from the regular adhesive hairs (Foelix & Erb 2010). Their hair shaft is rather smooth and lacks the many flared extensions ("end feet") that provide the contact points for adhesion (Foelix & Chu-Wang 1975; Niederegger & Gorb 2006). The question now was what the function of these scopulate hairs in *Liphistius* might be, if adhesion could be ruled out. Since these hairs occur only in adult male spiders, it seemed likely that they are somehow involved with pheromones. They could either produce a male secretion (pheromone) that would act as a signal for the female, or these hairs could be chemoreceptors that would perceive the female pheromone. In order to solve this question, we inspected the scopulate hairs of male *Liphistius* spiders with transmission (TEM) and scanning electron microscopes (SEM). In particular, the examination of thin sections in the TEM should provide an answer as to whether these hairs are assoeiated with glandular or with sensory cells.

Whole mounts of isolated "scopulae" fragments from male *Liphistius desultor* Schiödte 1849 and *L. endau* Sedgwick & Platnick 1987 were used for light microscopy. Phase contrast was best suited for revealing the internal structure of scopulate hairs.

For SEM, we dehydrated alcohol-fixed material in a series of ethanol and acetone, then transferred it to HMDS (hexamethyldisilazane) for 15 min before air-drying on filter paper. Tarsi were mounted ventral side up on carbon-coated stubs, sputtered with gold, and examined in a Zeiss DSM 950 SEM.

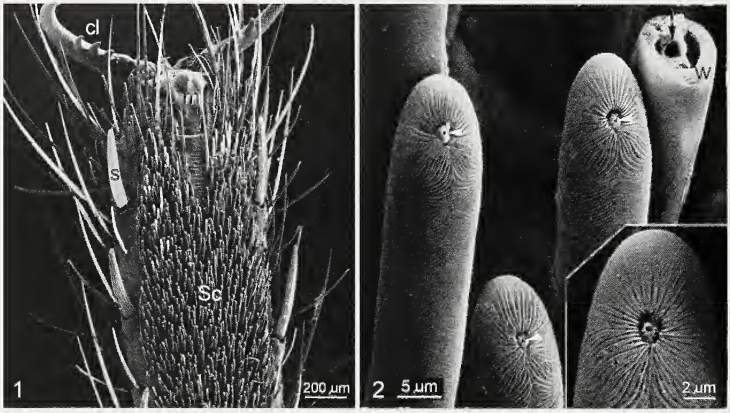
For TEM, tarsi from a male *Liphistius dangrek* Schwendinger 1996 were cut into small pieces, fixed in cold 5% cacodylate-buffered glutaraldehyde for 20 h, and post-fixed in 1% OsO_4 for 2 h. After dehydration in ethanol and propylene oxide, specimens were infiltrated with hard Epon overnight and then flat embedded and polymerized at 65° C. We then cut thin sections with a diamond knife, picked them up on Formvar-coated copper grids where they were contrasted with uranyl acetate and lead citrate for 10 min each. A Zeiss 9S2 and a JEOL TEM-1011 were used for fine structural examination.

The scopulate hairs in male *Liphistius* occur on the ventral tarsi, but not on the metatarsi. There is a marked difference in the number of these hairs between the different legs. Whereas the tarsi of the first pair of legs have only a distal hair pad of 150–200 hairs, the tarsi of the hind pair of legs are densely covered with 1,500–2,000 hairs.

Each tarsal hair pad is flanked laterally by a row of 6–8 curved spines (Fig. 1). A few tactile hairs are arranged serially in the midline of the hair pad, but there is no distinct division into two stripes as is the case in the scopulae of certain mygalomorphs.

Scopulate hairs are between 130–160 µm long and 10–14 µm in diameter (Figs. 2, 3). The base of the hair shaft is movably inserted into a socket (Fig. 4), and the distal end is blunt and slightly curved toward the leg surface. At low magnification the hair shaft appears smooth, but at higher magnification (SEM) shows fine ridges running perpendicular to the hair axis. Near the round tip of the hair, these ridges converge toward a small pore of 0.3–0.4 µm diameter (Fig. 2). This pore is always located subterminally, about 8–10 µm away from the tip, on the ventral side. While the pore opening is easily seen with the SEM, it is hardly detectable in the light microscope. However, under phase contrast microscopy, a thin central canal is visible inside the hair shaft, which begins at the distal pore, traverses the center of the hair shaft and terminates about 30 µm above the hair base (Figs. 3, 4).

Cross-sections of scopulate hairs show a solid, thick wall (2–3 µm) and a lymph-filled lumen (Fig. 5). The cuticular central canal has a much thinner wall (about 0.5 µm) and is filled with a rather dense lymph (Figs. 5, 6). More importantly, this central canal encloses many fine nerve fibers. The average number of these dendrites is 16, rarely 18–20. Their diameter is only 0.1–0.2 µm, and each dendrite contains only a few microtubules (2–9; Fig. 7). Closer to the hair base

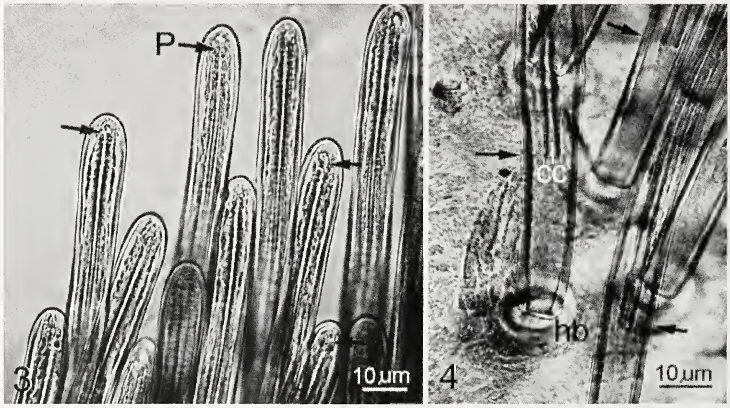


Figures 1, 2.—Ventral side of a tarsus in a male *Liphistius endau*. 1. The dense pad of scopulate hairs (Sc) is flanked by stout spines (S). Two main claws (cl) and a short middle claw (m) are seen on top. 2. Close-up of several scopulate hairs, ventral view. The hair shaft bears fine cuticular ridges, which converge toward a small, subterminal pore (arrow heads). One hair shaft is broken and reveals a rather thick hair wall (w) and a circular central canal (arrow) in the lumen. *Inset*: Pore and cuticular ridges at higher magnification.

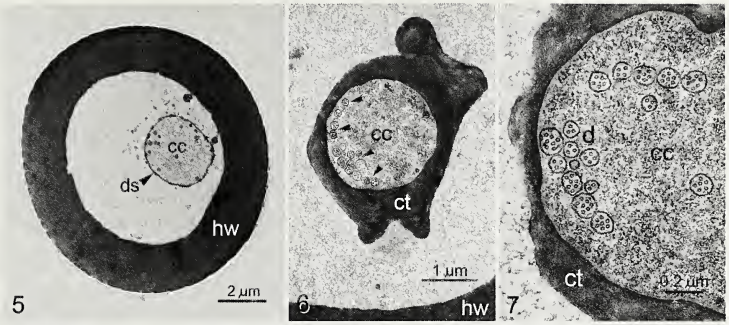
where the central canal ends (Fig. 4), the dendrites are encased by a very thin layer of extracellular material, the dendritic sheath (Fig. 5). At present we do not know yet whether there are any dendrites terminating at the base of the hair shaft, which would indicate an additional mechanoreceptive function.

Considering that there are at least 16 sensory cells per scopulate hair and the fact that one tarsus may be covered by 1,500–2,000 scopulate hairs (Fig. 8), there must be an enormous number of sensory nerve fibers in each tarsus. Indeed, cross-sections of a tarsus show two substantial sensory nerves (Fig. 9), but the exact number of nerve fibers (axons) cannot be determined in the light microscope due to their small diameter (mostly 0.1–0.2 µm). However, a few large axons of more than 10 µm in diameter can be seen with the light microscope (Fig. 10). They are reminiscent of the giant fibers known from other ancient arachnids e.g., in amblypygids (Foelix 1975). However, further studies using TEM are needed to confirm the presence of such giant fibers and associated synaptic connections.

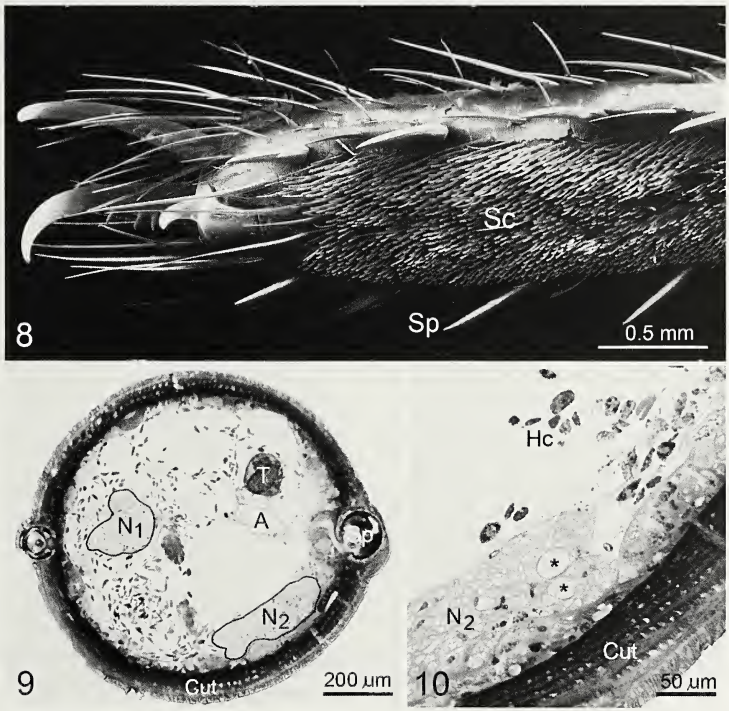
Finally, it was brought to our attention (Schwendinger pers. comm.) that "scopulae" restricted to adult males also occur in certain mygalomorph spiders (e.g., among the Idiopidae). For comparison we looked at one representative, *Idiops pylorus* Schwendinger 1991, and found very similar tarsal hair pads as in *Liphistius* (Fig. 11). Again, these scopulate hairs lack the highly branched structure of the common scopula (adhesive) hairs, and the smooth hair shaft bears the



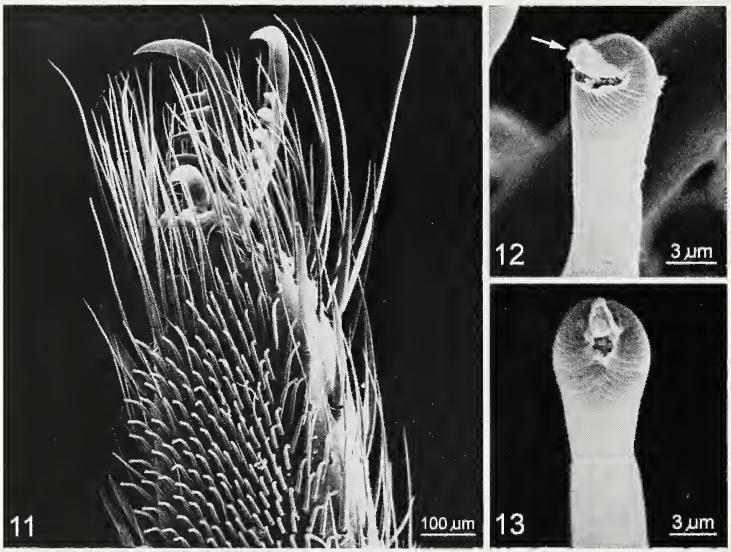
Figures 3, 4.—Scopulate hairs from a male *Liphistius desultor*, as seen in a wholemount. 1. The hair shaft contains a central canal that terminates in a small pore (P, arrows) just before reaching the blunt tip of the hair. 4. The basal region of scopulate hairs exhibits a distinct socket at the hair base (hb) and the beginning central canal (cc) about 30 µm above the hair base (arrows).



Figures 5–7.—Cross-sections of scopulate hairs. 1. In basal region, the hair wall (hw) is relatively thick, while the central canal (cc) is enclosed by a thin dendritic sheath (ds). The fine nerve fibers inside the central canal are barely visible at this low magnification. 6. In midregion the hair shaft shows that the dendritic sheath has been replaced by a massive cuticular tube (ct). Small nerve fibers (arrowheads) are apparent in the left half of the central canal (cc). 7. High magnification of the central canal (cc) reveals about 16 small dendrites (d) containing 2–9 microtubules each. Note the different density of the hemolymph inside and outside of the central canal (cc).



Figures 8–10.—8. Tarsus 4 in a male *Liphistius desultor*, ventrolateral view. About 800 scopulate hairs (Sc) were counted on this distal portion; the entire tarsus contains about 1,750 of these sensory hairs. Sp = lateral spine. 9. Cross-section of a tarsus in *Liphistius dangrek*. The hair bases of two spines (Sp) are located laterally in the thick leg cuticle (Cut). Two sensory nerves (N_1, N_2) comprise the axons of all the tarsal sensory hairs. A = leg artery, T = tendon of claw muscles. 10. Detail of a cross-sectioned sensory nerve (N_2) showing many small axons and two "giant fibers" (asterisks) of more than 10 µm in diameter. Hc = hemocytes (blood cells).



Figures 11–13.—Tarsus of a male *Idiops pylorus*. 11. Ventro-lateral view. Note the pad of scopulate hairs directly below the three tarsal claws. 12. The tip of these scopulate hairs shows an overhanging cuticular hood (arrow) that conceals the pore underneath. 13. A straight ventral view of the hair tip reveals the pore opening under the tongue-like hood.

same delicate ridges. The only morphological difference is that the subterminal pore opening is covered by a cuticular flap or hood (Figs. 12, 13).

There are two remarkable features about the scopulate hairs in *Liphistius* : 1) these hairs differ from the common adhesive hairs of scopulae found in other spiders (e.g., in tarantulas), and 2) these scopulate hairs occur only in the adult male spiders but not in females or juveniles.

The structure of these scopulate hairs is very similar to known contact chemoreceptors in arthropods, especially in spiders (Foelix 1985a). The most convincing evidence for chemoreception is the presence of numerous small dendrites lying inside the hair shaft; most likely, they are exposed to the environment at the pore opening below the tip. The number of dendrites is similarly high (16), as in the regular chemosensitive hairs of spiders (19) (Foelix 1970; Foelix & Chu-Wang 1973; Harris & Mill 1973). It is noteworthy that the "regular," S-shaped taste hairs are also present in *Liphistius*, usually in rows on the dorsal side of the tarsus but also interspersed among the hundreds of ventral scopulate hairs. Perhaps those regular taste hairs are more generalized chemoreceptors, whereas the scopulate hairs are more specialized (e.g., for the detection of female pheromones). This interpretation is supported by the fact that scopulate hair pads occur only in adult male spiders. Indirect support comes from behavioral observations: males can apparently differentiate trap doors from receptive females and from juveniles – only the former are approached during courtship, whereas the latter are ignored (Haupt 2003).

The exclusive occurrence of scopulate hairs in the male is not restricted to *Liphistius* species, but has also been noted in several mygalomorph families; e.g., in Actinopodidae, Antrodiaetidae, Atypidae, Ctenizidae, Cyrtaucheniidae, and Idiopidae (Raven 1985). Indeed, in *Idiops pylorus*, we have found the same type of scopulate hairs as in *Liphistius* (Figs. 11–13). This widespread occurrence indicates that the presence of scopulate hairs may be an ancient (plesiomorphic) character that is shared by the Mesothelae and many Mygalomorphae. Until now these scopulate hairs have not been reported in the literature on Mesothelae (Haupt 2003); in Mygalomorphae they were only used for classification, but without any indication of their possible function (Raven 1985).

A remaining question is why a male spider would need several thousands of such scopulate hairs. We counted about 1,750 scopulate hairs on a single tarsus (leg 4), which corresponds to 28,000 nerve fibers just for the sensory input of scopulate hairs from one leg. This is even more than the entire sensory input found in the antenniform legs of amblypygids (about 20,000 nerve fibers; Foelix & Troyer 1980; Foelix et al. 2002). It seems that *Liphistius* also has a similar system of giant fibers (Fig. 10) and associated synapses, as was found in amblypygids and other arachnids (Foelix 1975, 1985b; Fabian-Fine et al. 2000, 2002), but this needs to be clarified with further ultrastructural studies.

Finally, the extremely high sensory input from thousands of chemoreceptors is also baffling when we consider the short time span during which it can actually be used: adult *Liphistius* males die only a few weeks after their final molt (Schwendinger pers. comm.); perhaps the wandering males need to optimize the chance of finding a female during that brief time.

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General: The *Journal of Arachnology* publishes scientific articles reporting novel and significant observations and data regarding any aspect of the biology of arachnid groups. Feature articles and short communications must be scientifically rigorous and report substantially new information. Submissions that are overly narrow in focus (e.g., local faunal lists), have poorly substantiated observational data, or that present no new information will not be considered.

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